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Abstract

This thesis investigated social learning mechanisms and strategies relating to the characteristics of a model (the individual transmitting the information) and the prior experience of an observer (the individual acquiring the social information) in children and chimpanzees. Experimental designs that mirrored naturalistic settings enabled an investigation of how social learning mechanisms and strategies were affected by: (1) the characteristics of a model, (2) the prior experience of an observer, (3) continued model demonstrations and (4) repeated observer interactions with the task. If models provided viable novel solutions then their characteristics seemed ineffectual upon children's copying of these solutions. Yet the characteristics of the model did influence children's copying of irrelevant actions; children who observed an adult reproduced more causally irrelevant actions than those who observed a child. Furthermore, when a known peer with higher, rather than lower, past-proficiency matched a child's original solution the child was more likely to continue using this solution. Chimpanzees were biased towards touching the tool seeded by a known conspecific with higher, rather than lower, past proficiency but this bias did not affect which tool a chimpanzee successfully used. Both species showed an ability to learn multiple demonstrated methods of success within their corresponding tasks and to explore beyond demonstrated methods. It is argued that both species show more task-behavioural flexibility than previously thought and the implications for this in terms of cultural evolution are discussed.

**The influence of model-based biases and observer
prior experience on social learning mechanisms and
strategies**

Lara Wood

Thesis submitted for the degree of Doctor of Philosophy

Durham University Psychology and Anthropology Departments

2013

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Declaration

A portion of data contained in chapter III of the thesis has previously been submitted for a master's degree at Durham University. Additional data collection, analysis and interpretation of the complete data set in chapter III, alongside all other material, has not previously been submitted by me for a degree in this or in any other institution. If material has been generated through joint work, my independent contribution has been clearly indicated. In all other cases material from the work of others has been acknowledged and quotation and paraphrases suitably indicated.

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This thesis is dedicated to great apes.

Chapter I

Introduction

Humans stand alone in the breadth, stability and complexity of their culturally learnt behaviour. This cultural supremacy is underpinned by social learning; the transmission of information from one or more individuals to another. Humans, however, are not unique in their ability to learn socially. From insects (Leadbeater & Chittka, 2007) to man's closest living relative, the chimpanzee (Whiten, Custance, Gomez, Teixidor & Bard, 1996), non-human animals (henceforth animals) show a range of social learning abilities. In order to understand our species' culture we must understand the social learning mechanisms (Heyes, 1994; Whiten & Ham, 1992) and strategies (Laland, 2004) that might influence cultural behaviour, its stability and its evolution (Mesoudi, Whiten, & Laland, 2006; Whiten, Hinde, Laland, & Stringer, 2011). Two ways of achieving this are: (a) compare the abilities of various other species, both closely and distantly related to us in evolutionary history. This *comparative psychology* may reveal behavioural similarities or dissimilarities and allow an investigation of the cognitive processes behind such behaviour and, potentially, its evolutionary origins. And (b) study the ontogeny of our species. Such *developmental psychology* allows an investigation into the acquisition of social learning mechanisms, strategies and the co-developing cognitive skills which facilitate their use.

The overarching aim of this thesis is to investigate social learning mechanisms and strategies. Specifically, the characteristics of a model (the individual emitting the information) and the prior experience of an observer (the individual acquiring the social information) were investigated in relation to the observer's social learning strategies, mechanisms and behaviour changes with continued task demonstrations and

interactions. A developmental and comparative approach is taken, separately, by investigating these strategies and mechanisms in four- to six-year-old children and captive chimpanzees. The following sections define and expand upon the terminology used throughout this thesis as well as introducing the main theoretical concepts and experimental methods.

Social Learning Mechanisms

Learning can occur either with or without social information. Without-social-information (asocial) learning could be reliable because individuals personally sample their environment but it is time consuming and laborious. Social learning prevents these personal costs but the information provided may be unreliable or outdated (Laland, 2004). Investigating established mechanisms of social information transmission aid our understanding of animals' learning processes. Here, mechanisms refer to behavioural outcomes rather than specific cognitive processes (Heyes, 2012). The plethora of social learning mechanisms have been outlined by Whiten and Ham (1992), Whiten, Horner, Litchfield, and Marshall-Pescini (2004) and Whiten, McGuigan, Marshall-Pescini and Hopper (2009, Figure 1). As can be seen in Figure 1, there are many potential mechanisms for information transfer and those presented in the figure are, by the original authors own admission, not exhaustive. There is also debate about the exact definitions of some mechanisms, such as imitation (Whiten et al., 2009). Indeed, as research continues, subtle differences within each mechanism (e.g. emulation) have been discovered so that this mechanism becomes an umbrella term for a number of different mechanisms (e.g. object movement re-enactment, goal emulation, result emulation; as highlighted by Hopper 2010). Therefore, it is important to outline and define the mechanisms of interest throughout this thesis.

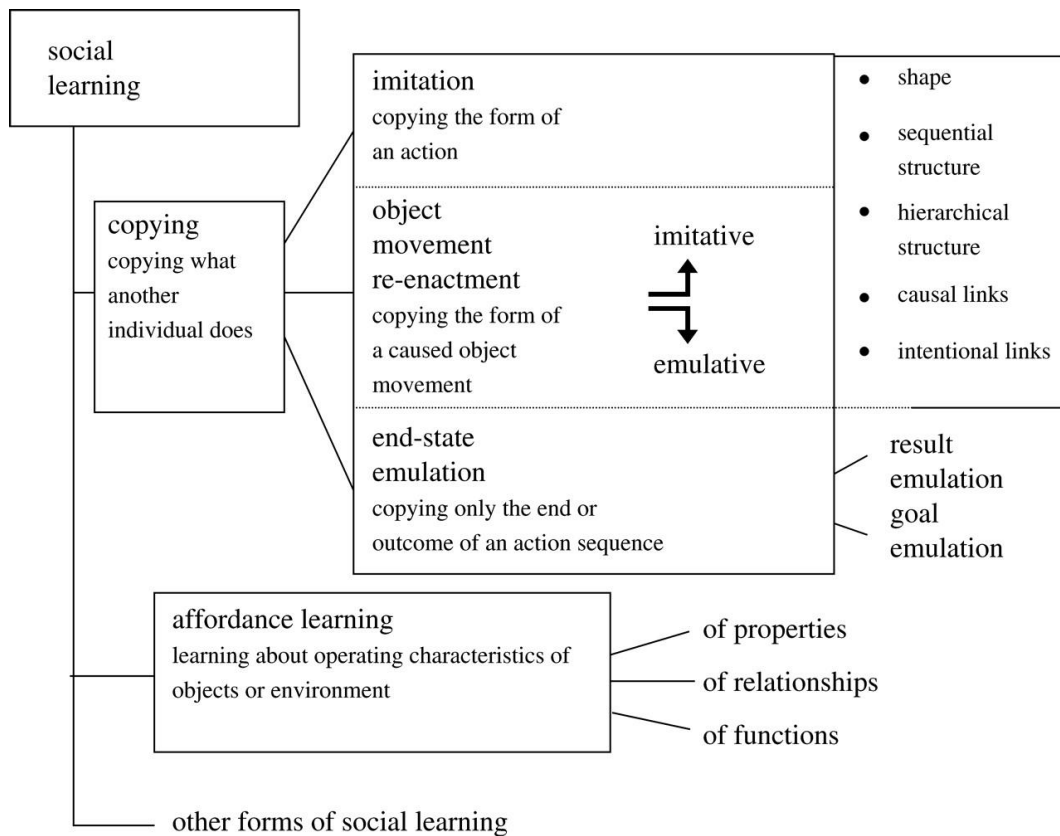


Figure 1. From Whiten et al. (2009, p.2148) with permission. See also Whiten et al. (2004) and Whiten & Ham (1992).

In this thesis three social learning mechanisms are of interest; stimulus enhancement, goal emulation and imitation. These terms are operationalized as follows:

(1) *Stimulus Enhancement*: an increase in the probability that the observer will interact with stimuli of the same physical type as those with which the demonstrator interacts, followed by asocial learning (Heyes, 1994). Typical evidence for this would include an individual touching an artefact following watching a model interacting with that artefact more than an individual who has not witnessed a social interaction with the object. Stimulus enhancement differs from local enhancement, whereby a learner's attention is drawn to a location by another individual. (2) *Goal Emulation*: the observer learns from an individual that a goal can be achieved (Whiten & Ham, 1992). Typical evidence for this would be that an observer who witnesses another individual achieve a goal is

successful at completing the same goal but does not necessarily use the same method as the original model. (3) *Imitation*: an observer reproduces specific aspects of the intrinsic form of an act from the observation of a model (Whiten & Ham, 1992). Typical evidence for this would be that individuals are more likely to reproduce specific actions or methods in the same manner as they have witnessed. Copying of this fidelity can lead to the reproduction of inefficient or unnecessary actions, sometimes referred to as overimitation (Lyons, Young, Keil, 2007). Throughout this thesis use of the term ‘overimitation’ will be avoided as it implies that the fidelity resulting in imitation of causally irrelevant actions is maladaptive, when in general this may not be the case. Instead, ‘high-fidelity’ imitation is used.

It is important to note that mechanisms are not mutually exclusive within species. An animal species could use different mechanisms in different contexts. For example, Nagell, Olguin & Tomasello (1993) found that chimpanzees were more likely to obtain out-of-reach food with a tool after a social demonstration of that tool than with no information. The chimpanzees with a social demonstration did not imitate the precise two-action step of the model, suggesting an absence of behavioural imitation but a presence of goal emulation. In other circumstances chimpanzees may copy the exact actions employed by models during reward retrieval (Whiten, et al., 1996; Whiten, Horner & de Waal, 2005; Whiten et al., 2007). Chimpanzees, like other animals, might employ ‘a portfolio of alternative social-learning processes in flexibly adaptive ways, in conjunction with non-social learning’ (Whiten, et al., 2004, p. 36). Even within the same context a series of mechanisms could underpin the socially learned behaviour. For example a demonstration involving multiple components and steps might result in some aspects being imitated whilst others are emulated.

Social Learning Strategies

Laland (2004) argued that social learning should not be considered inherently adaptive, but as a source of information that may or may not be used, dependent upon context. Accordingly, theoretical models of cultural evolution predict the evolution of flexible strategies (or transmission biases) enabling avoidance of unreliable or redundant information, and influencing the circumstances under which individuals copy others and from whom they learn (Boyd & Richerson, 1985). Implementation of these strategies may not only dictate whether social information is copied or not but which, of a variety of social demonstrations witnessed, might be most likely to be copied (Mesoudi, 2008; 2011; Mesoudi & O'Brien 2008). The use of such cues in guiding behaviour is thought to increase fitness more than individual learning (Mesoudi & O'Brien, 2008) or unbiased social learning in which individuals acquire variants according to the frequency at which they are practiced (Rendell et al., 2011).

Transmission biases refer to information, which has the potential to be socially learnt, being influenced by someone or something. Thus, a bias influences the likelihood of the social transmission of information. In the last decade there has been a surge of activity directed at identifying and understanding the variety of biases that might influence social learning (Kendal, Coolen, van Bergen, & Laland, 2005; Morgan, Rendell, Ehn, Hoppitt, & Laland, 2012; Rendell, et al., 2011; see Figure 2). There are biases that relate to the content of the social information, sometimes referred to as 'what' biases (Mesoudi & Whiten, 2008; Mesoudi, Whiten & Dunbar, 2006), direct biases (Boyd & Richerson, 1985) or content biases (Henrich & McElreath, 2003). Alternatively, there are biases which relate to the context of the social information (context dependent biases; Henrich & McElreath, 2003), which can relate to the state (state based; Rendell, et al., 2011) of the observer, such that individuals may copy if

their personal information is outdated (as seen in fish; van Bergen, Coolen, & Laland, 2004) or if they are dissatisfied or uncertain (as seen in fish; Kendal, Coolen, & Laland, 2004; Kendal, Rendell, Pike, & Laland, 2009). Context dependent biases can also relate to the frequency of the behaviour whereby individuals glean information regarding the level of incidence of behaviours (frequency-dependent biases; Boyd & Richerson, 1985; Day, MacDonald, Brown, Laland, & Reader, 2001) such that individuals may copy the most frequently displayed behaviour (Toelch, Bruce, Meeus, & Reader, 2010). Finally, context can relate to the characteristics of the model, whereby certain models provide more reliable, and thus adaptive, information than others. These potential biases have been termed ‘who’ biases (Laland, 2004), indirect biases (Boyd & Richerson, 1985) and context dependent *model-based biases* (Henrich & McElreath, 2003). Much of the thesis revolves around investigating such biases in children and chimpanzees.

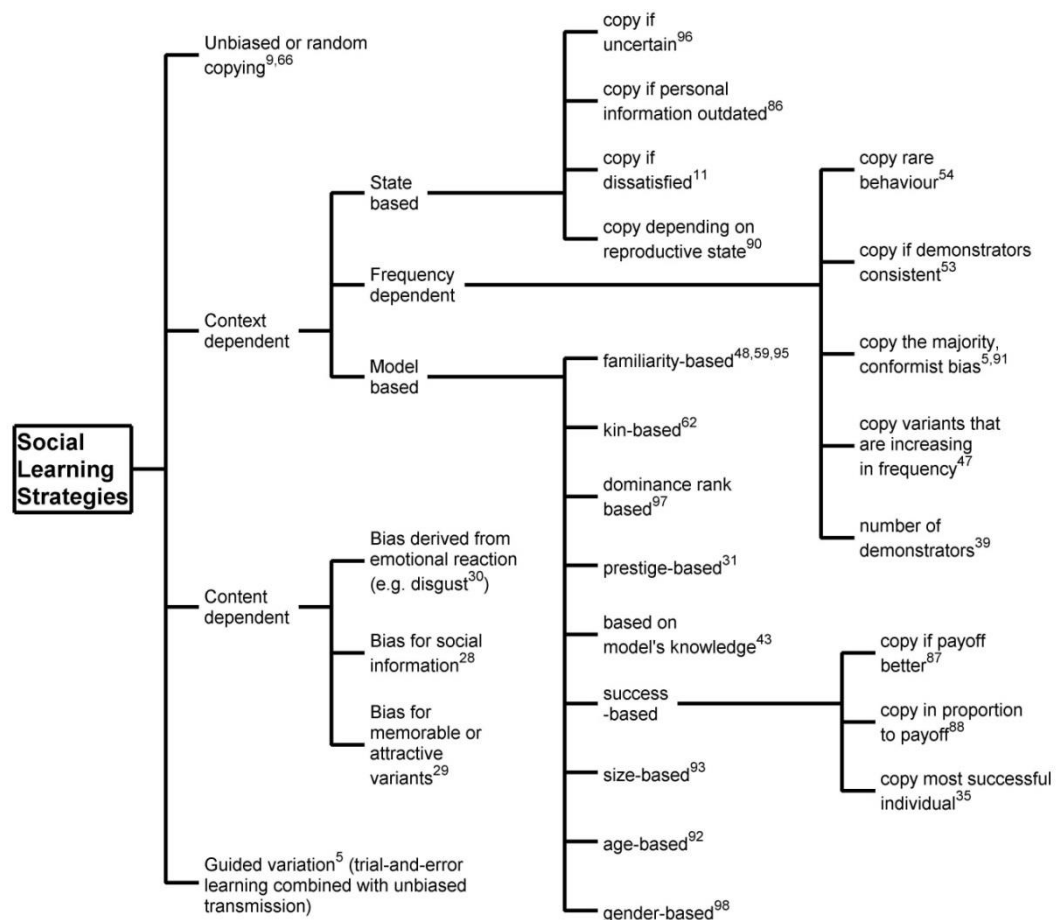


Figure 2. From Rendell et al. (2011, P.71) with permission.

Model-based Biases

Models have different characteristics that might influence the likelihood of copying the behaviour they demonstrate. These may include, but are not limited to, a model's previous performance (Koenig, Clément & Harris, 2004), knowledge state (Jaswal & Malone, 2007), age (Jaswal & Neely, 2006; Rakoczy, Hamann, Warneken, & Tomasello, 2010), sex (Frazier, Gelman, Kaciroti, Russell, & Lumeng, 2011) and social status (Chudek, Heller, Birch, & Henrich, 2012). Furthermore, observers' own characteristics may influence who is the 'best' model for them. For example, individuals might be biased towards learning from those from a similar, rather than different, cultural background because they are motivated to learn culturally appropriate behaviour (Kinzler, Corriveau, & Harris, 2010). Such an interaction between observer and model characteristics emphasises the role of heuristics or transmission biases in enabling the most appropriate model, potentially providing the most useful and adaptive behaviour, to be copied.

The main focus of this thesis is model-based biases. I begin by producing a comprehensive literature review (Chapter II) detailing the adaptive value of model-based biases in children's learning. This review also touches upon the literature in other animals such as chimpanzees. Following on from this, model-based biases in children and chimpanzees' learning are investigated separately. As the thesis is in publication format, the theoretical underpinning for each specific paper is discussed in more detail in each chapter.

Prior Experience

When learning about artefacts, individuals do not have just demonstrations of the same solution from a single model followed by an opportunity to interact with that artefact (as has been used in some social learning studies; Flynn & Whiten, 2008a; Horner & Whiten, 2005). Interspersing personal experience and varied demonstrations might have a significant impact upon children's learning strategies and the social learning mechanisms they employ. For example individuals might copy all observed actions faithfully until they have a chance to interact with the task themselves and discover which actions are causally necessary and unnecessary, a 'copy now, refine later' strategy (Whiten et al., 2005). Here, a first interaction might involve high-fidelity imitation of actions but a second interaction might omit irrelevant actions. Alternatively, a first interaction may involve goal emulation but with continued demonstrations individuals might increase their copying fidelity of the model. Both these outcomes might tell us something very important about the way in which individuals socially learn and, therefore, it is important to give individuals multiple demonstrations and chances to interact with a task.

Over time, individuals might also witness alternative methods of achieving a goal. For example, a model could demonstrate one method, the observer then interacts with the task and then the same or different model could demonstrate an alternative method. When faced with divergent information (e.g. Kendal et al., 2004) it would be adaptive to select and reproduce the information most suited for one's needs or the current context. However, there may be occasions when all the methods one experiences (personally or socially) are equally viable. When this occurs, the sequence of the information's acquisition could influence which solution is selected. Individuals may be biased to the first method they witness due to a primacy (Murdock, 1962) bias or

because once they have a reliable solution, acquiring other information is unnecessary or inhibited (Hopper, Flynn, Wood & Whiten, 2010). Alternatively, individuals could be biased towards the most recent information because of a recency (Murdock, 1962) bias or because it is the most reliable information pertaining to a potentially changing environment (e.g. Van Bergen et al., 2004).

Alternatively, individuals could witness alternative interactions from different models. If both solutions look viable individuals' choices of whom and what they imitate could be guided by the model's characteristics. There may also be an interaction between the sources of the information (personal versus socially demonstrated by model/s) and the content of information influencing solution choice but also the mechanism employed in copying. For example, infant imitation of parents is more likely to consist of motor skills (e.g. tool use) whereas affective behaviours are imitated from siblings and peers (Kuczynski, Zahn-Waxler, Radke-Yarrow, 1987). Also, four- to five-year-old children imitate adults more than children and same age peers when an action is novel, but copy a peer over an older child and adult when the action is not novel (Zmyj, Daum, Prinz, Nielsen, & Aschersleben, 2011). In the first context, the function may be to learn a new skill whereas in the second context the action is familiar. Each context may affect the implementation of a model-based bias.

Finally, an individual could have an opportunity to interact with a task *before* they witness social information pertaining to it. Here, individuals may be biased towards the method they personally acquired because they have experience of its reliability (e.g. a strategy of 'copy only when uncertain' as seen in a variety of animals: Kendal et al. 2005). Alternatively a bias towards social information may supersede prior personal information.

All these scenarios reflect realistic ways in which information about artefacts is learned. Therefore, it is important to investigate the impact of multiple model demonstrations and observer interactions, as well as repeated interaction with artefacts, on children's social learning strategies and mechanisms. It is this level of ecological validity that is aimed for in the empirical chapters of this thesis.

Overview of Experimental Methods

Participants

Human culture accumulates “refinements over time, thereby producing both technology and other cultural achievements of astonishing complexity and diversity unprecedented in the rest of nature” (Dean, Kendal, Schapiro, Thierry, & Laland, 2012, p.1114). Understanding our uniquely cumulative culture requires a comparative approach. For example, Tennie, Call & Tomasello (2009) argue that chimpanzees and humans have different cognitive and learning mechanisms resulting in chimpanzee populations failing to show cumulative culture. Instead, chimpanzee cultures reflect traditions involving behaviour patterns that are within the species' existing cognitive repertoire. This difference, they argue, is caused by species' differences in attention to demonstrations and uniquely human cooperation. Building on this, Whiten & Erdal (2012) claim that cooperation, along with mindreading (Theory of Mind), language and egalitarianism creates a species-unique socio-cognitive niche, as supported by recent empirical work (Dean et al., 2012). To investigate these claims it is useful to consider human development and comparative evidence. The empirical work in this thesis focusses on two populations, human children and adult chimpanzees. These two populations will not be directly compared in this thesis. Instead, study of each

population tells us about their specific skills and informs our understanding of human culture.

Children

To investigate human social learning and accompanying socio-cognitive skills it is useful to look at children's development (Herrmann, Call, Hernández-Lloreda, Hare & Tomasello, 2008). The majority of this thesis focusses on children's social learning mechanisms and strategies including a detailed review (Chapter II) of the adaptive value of model-based biases and the requisite cognitive skills associated with such biases. As such, a detailed description of children's social learning will not be given here. In essence, children are cultural magnets (Flynn, 2008) and their social learning abilities are a window onto human cultural supremacy; children are able to imitate the actions of a model upon a novel artefact from infancy (Meltzoff, 1985), copy a complex set of nine actions upon a task by three years (Flynn & Whiten, 2008b) and generally acquire an innumerable amount of artefact, language and culturally-appropriate customs and norms. The aim of the thesis is to explore this social learning in more depth. All children tested were between four and six years of age, allowing for comparison with a large body of work investigating social learning strategy and mechanisms conducted with children (e.g. Flynn & Whiten 2008a, 2008b; Horner & Whiten, 2005; Koenig & Harris, 2005; McGuigan, et al., 2007, 2011). Furthermore children of this age were selected as they have an understanding of age and knowledge state (Edwards, 1984; Wellman et al., 2001) and they will have been in an educational environment with known peers for a stable amount of time.

Chimpanzees

Chimpanzees are humanity's closest living relative (Prüfer, et al., 2012). Popular literature (de Waal, 2007) and academic study (Tomasello, Call & Hare, 2003) have effectively argued that chimpanzees share many of our cognitive and socio-cognitive skills. This includes a portfolio of social-learning mechanisms (Whiten, et al., 2004). For example, like human neonates (Meltzoff & Moore, 1977), chimpanzees are able to imitate human demonstrated facial gestures (Bard, 2007) and young chimpanzees are capable of imitating arbitrary actions performed by a known caregiver (Custance, Whiten & Bard, 1995). Adult chimpanzees are also able to socially learn a number of complex tool-use behaviours (Whiten et al., 2007). Indeed, in certain contexts chimpanzee's social learning mechanisms can appear more efficient than humans (Horner & Whiten, 2005). In addition, as with children (Gergely, Bekkering & Király, 2002), chimpanzees exhibit 'rational imitation' (Buttelmann, Carpenter, Call and Tomasello, 2007) whereby when the models use unusual body parts to switch on a display chimpanzees are more likely to copy the unusual action when the model's hands are free as opposed to constrained.

This ability to socially learn is not unique to captive individuals; chimpanzees in the wild demonstrate clear behavioural patterns unique to chimpanzees within their geographical location (Whiten et al., 1999) ultimately developing group differences. For example, one method of ant-dipping is customary at Gombe but not in any other site while a second distinct method is customary in Bossou and the Tai Forest but absent elsewhere. These differences appear to be independent of ecological and genetic differences although see Laland & Janik (2006) for a discussion of why claims of animal cultures remain controversial.

What chimpanzees learn when observing others, i.e. the mechanisms of the transmission of social information, is still a matter of some debate (Whiten et al., 2009). Also, the extent to which chimpanzees use heuristics to guide when, and from whom, they socially learn (Laland, 2004) as other animals do (Kendal et al. 2005) has, to date, been little investigated. To understand differences in human and chimpanzee social learning we need to further explore these mechanisms and strategies. The aim of the chimpanzee study in this thesis (chapter VI) was to implement an experimental design which mirrored captive chimpanzees' naturalistic settings to test learning mechanisms and model-based biases. Previous work has demonstrated that chimpanzees preferentially copy the choices of older, higher ranking and previously proficient models (Horner, Proctor, Bonnie, Whiten, & de Waal, 2010) although it is not known whether it was the age, dominance and/or past proficiency that influenced the chimpanzees' choices. Here, the effect on chimpanzees' behaviour of a model-based bias pertaining to known conspecifics' past proficiency was investigated. In chapter V the same question is investigated in children but using a modified study design which mirrored their school setting.

Furthermore, in adopting the study design outlined earlier, of multiple interactions with task, the thesis addresses a theoretical conflict which is particularly pertinent to the chimpanzee culture literature. The issue pertains to whether chimpanzees remain conservative to an initially discovered method of achieving a goal (Hopper, Schapiro, Lambeth & Brosnan, 2011; Hrubesch, Preuschoft, & van Schaik, 2009; Marshall-Pescini & Whiten, 2008) or are able to flexibly investigate alternative solutions despite a prior successful solution (Dean et al. 2012). Although not quite the same context, wild chimpanzees' use of a sequential 'tool-kit' to obtain honey (Sanz & Morgan, 2007; Yamamoto, Humle & Tanaka, 2012) potentially indicates such

flexibility. The study with chimpanzees presented here extends previous research by introducing two task solutions simultaneously. This means that potentially the chimpanzees can make choices of which solution to attempt first and whether they incorporate both solutions into their repertoire.

Tasks

Comparing behaviour (such as reward retrieval) of individuals with social information with those who have no social information reveals the presence of social learning. However, such a comparison cannot necessarily identify which mechanisms might be underpinning the social learning. For example, the model may have merely drawn the observer's attention to the artefact (stimulus enhancement) and subsequent actions were asocially learnt. To overcome this Whiten et al. (1996) adopted a two-action task design first implemented by Dawson & Foss (1965). Whiten et al. (1996) created a food processing task as this was deemed the most likely domain in which behaviour would be socially transmitted naturally. Whiten et al. (1996) called these kinds of tasks 'artificial fruits'. The value of these tasks is exemplified by a number of studies, which have used a Glass Ceiling Box (GCB) artificial fruits task. This task involves a transparent or opaque box with a hole at the front that can be revealed by sliding or lifting a door. The goal is to retrieve a reward from a tube located behind the door by inserting a stick tool into the tube. The demonstrated actions directed to the door are causally necessary to retrieve the reward. However, the GCB has a further opening in the roof, covered by a two-bolt defence that can be removed by poking or dragging them from the opening with the stick tool. This hole leads to an empty compartment with a 'glass ceiling' preventing physical access to the reward, so actions directed to the bolts or the upper compartment are observably (when the box is

transparent) or unobservably (when the box is opaque) causally irrelevant to retrieving the reward.

By changing the context (i.e., the availability of causal information) social learning mechanisms can be investigated (Horner & Whiten, 2005; McGuigan, et al., 2007). For example, when chimpanzees observed a human demonstrate the irrelevant ceiling actions and relevant door action in the opaque condition, they reproduced both the relevant and irrelevant actions, thus showing high-fidelity imitation of all the actions witnessed. However, with the transparent GCB chimpanzees ignored the irrelevant actions instead and imitated only the relevant actions (Horner & Whiten, 2005). The GCB was also presented across species. Horner and Whiten (2005) found that whilst three- to four-year old children showed a similar pattern of behaviour to the chimpanzees in the opaque condition, when the box was transparent children continued to imitate the irrelevant ceiling actions. Lastly, developmental changes in social learning mechanism use in a single species have also been tracked. McGuigan et al. (2007) found that both three- and five-year-old children imitated the irrelevant actions regardless of the availability of causal information following a live demonstration. However, when the information available was degraded in a video demonstration, the 3-year-olds did not employ high-fidelity imitation and omitted irrelevant actions but the 5-year-olds continued to employ a high-fidelity imitative approach, copying irrelevant and relevant actions. This propensity to imitate clearly irrelevant actions continues into adulthood (Flynn & Smith, 2012; McGuigan, Makinson, & Whiten, 2011). Whilst these experiments focus on a single task they assist in our understanding of what mechanisms might underpin the spread of behavioural traditions. For example, the difference between children and chimpanzees might indicate that chimpanzees attend preferentially to goals and results, and children attend, to a greater extent, to the actions

being performed by the model. This may result in children learning functionally irrelevant but potentially culturally relevant behaviours (Horner & Whiten, 2005; Tomasello et al., 1993).

For children, artificial fruits that contained a reward (sticker) held in place by a series of defences were used. Using a task with multiple possible solutions allowed a number of distinctions to be identified: (a) the propensity to discover each of these solutions during personal exploration, (b) the level of replication of a demonstrated solution compared to the level of production of an alternative solution, (c) fidelity or exploration of solution use once an alternative solution was demonstrated and (d) the replication of irrelevant actions under varying contexts. For chimpanzees, a task involving an inaccessible reward (food that was out of reach) with two physically and functionally unique tools was created. This also enabled an investigation of: (a) the propensity to discover each of these solutions during personal exploration, (b) the level of replication of a demonstrated solution compared to the level of replication and/or innovation of an alternative solution.

Experimental Design

Experimental work on social learning in children has almost exclusively used a dyadic design, in which a single naïve (no prior experience with the task) child participant watches another individual (normally an unfamiliar adult) perform a behaviour directed at the task and then is given the opportunity to interact with the task apparatus, to discover whether he or she will perform the behaviour, or variants of the behaviour, witnessed. These dyadic studies are extremely informative because the experimenter has complete control of the social demonstration that the child receives, with regard to the number of demonstrations as well as who demonstrates and what

(method and inclusion of irrelevant actions) they demonstrate. For this reason, the experiments with children presented in this thesis use this dyadic design but with a number of significant considerations and modifications. First, the identity of the model is considered with the model being either as neutral as possible (a hand puppet) or a model with a specific characteristic and made these characteristics the focus of the study. Second, in certain conditions children were able to explore the task before receiving social information, offering a more naturalistic scenario of learning. Third, under certain conditions children were provided with alternative social information from either one or more models. Fourth, children were given up to seven interactions with the task allowing an investigation of continuation of fidelity. These modifications meant model-based biases and behavioural change could be investigated while maintaining maximum control of the demonstrations.

An alternative to the typical dyadic design is the use of diffusion experiments. It is argued that diffusion experiments allow for greater external validity because they allow for the investigation of how behavioural variations spread and how faithfully they do so (Whiten & Mesoudi, 2008) in the natural context in which social transmission occurs - the group. One particular diffusion design, open diffusion, involves introducing or 'seeding' a task-behaviour into a naïve group using demonstration by a trained or naturally proficient model (Day, Coe, Kendal & Laland, 2003; Flynn & Whiten, 2010; Whiten & Mesoudi, 2008). With chimpanzees, open diffusion offers an additional benefit as, other than during the training of the model, individuals are not separated from group mates, thus reducing any potential stress involved in the study. By using multiple groups and counterbalancing methods, open-diffusion designs can be used to look at social learning mechanisms (Whiten & Mesoudi, 2008) and, potentially, strategies. Moreover, multiple methods have been developed recently to enable the

identification of social learning mechanisms and strategies in such naturalistic contexts (Kendal, Galef, & Van Schaik, 2010). Open-diffusion designs provide less experimental control, since participants choose when, or indeed whether, to attempt the task and the experimenter cannot control the content of each demonstration (and who provides it) or task interaction to the same degree as dyadic experiments. The resulting transmission of behaviour is thus potentially much messier (Flynn & Whiten, 2010). However, as open-diffusion represents a more ecologically valid context in which to explore social learning and cultural transmission a modified open-diffusion design with the chimpanzees was used.

Aim and Structure of this Thesis

The purpose of this thesis is to investigate model-based biases and behavioural change regarding the use of differing social learning mechanisms and strategies in children and chimpanzees. Chapter II reviews literature surrounding model-based biases in children's copying behaviour (including preference adoption), arguing that model-based biases are adaptive and that different biases require different cognitive and social-cognitive skills. Chapter III introduces an empirical study of children, investigating transmission biases relating to two model characteristics. Specifically, the age and stated knowledge state of a model was manipulated to investigate the fidelity of children's copying. Children were more likely to copy all of the actions presented by an adult model than a child model. This chapter also revealed that continued demonstration and interaction did affect imitation of irrelevant actions relative to model identity such that those who witnessed a knowledgeable model increased the number of irrelevant actions they performed more than those who witnessed an ignorant model. This behaviour change is explicitly tested in Chapter IV, an empirical study investigating

children's solution choice and social learning mechanisms following differing prior experiences and multiple social demonstrations. Children who acquired a solution either socially or asocially and then presented with an alternative solution that included irrelevant actions did not remain polarised to their initial solution. Rather, these children attempted the newly presented solution and then incorporated both solutions into their repertoire. Furthermore, children who acquired a solution through personally acquired information omitted subsequently demonstrated irrelevant actions to a greater extent than did children with prior social information.

The final two empirical studies investigate the interaction between a model-based bias of past-proficiency and multiple demonstrations and personal task interactions. Past-proficiency relates to a success model-based bias as outlined in Figure 2 (Rendell et al., 2011). A success model-based bias can refer to instances in which learning may be biased towards copying (a) if the payoff is better, (b) in proportion to the payoff or (c) the most successful individual. The first two instances refer specifically to the outcome of the behaviour whilst the third relates more to the characteristics of the model. However, it is unclear whether these instances are occurring in the present, (as the model is demonstrating the information which may be transmitted), or in the past (the success was demonstrated in the past and that some form of 'success reputation' is biasing subsequent information transmission). Furthermore, it is not clear whether success relates to domain specific model success relating to the specific information which is to be transferred or whether it is domain general success, i.e. that the model generally has more success in his/her environment, which may also be related to dominance and prestige (Henrich & McElreath, 2003). Therefore, we use the term past-proficiency to refer to a model's domain-specific ability shown in the past. As such it focusses on the potential for a model to have a reputation for being skilled within the

domain in which the model is currently demonstrating. Specifically, children (Chapter V) and chimpanzees (Chapter VI) were presented with demonstrations from known classmates/conspecifics, of differing proficiency ‘reputations’, regarding the use of one or other manipulandi/tool to retrieve a reward. These two studies were tailored to each species and their corresponding natural context, rather than attempting a direct comparison. The children were motivated to incorporate multiple solutions into their repertoire and this appeared to supersede a proficiency-reputation model-based transmission bias. However, when one model matched a child’s solution and one model offered an alternative solution children were biased towards selecting the solution choice of the model with the highest proficiency-reputation. Likewise, the majority of chimpanzees were able to use both tools and some chimpanzees asocially learnt new methods of reward retrieval. However, the first tool touched by chimpanzees from the model-groups indicates a model-based transmission bias as individuals were significantly more likely to match the tool demonstrated by the model with the higher past proficiency than the lower past proficiency. The thesis concludes (Chapter VII) by discussing transmission biases in relation to children and chimpanzees in the broader context of learning and cultural evolution.

Format of Chapters

The chapters presented here are in publication manuscript format. Before each chapter there will be a brief cover sheet, indicating the publication status of each paper. References contained in each chapter will be presented at the end of the corresponding chapter. Due to the ‘thesis by publication’ format there will be no General Methods chapter, the relevant background to the methods involved in the thesis having been covered in this chapter.

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Chapter II

Who do children copy?

Model-based biases in social learning

This chapter focusses on reviewing evidence for the adaptive value of model-based biases in children's learning. This chapter has undergone two rounds of peer-review in *Developmental Review* and has been invited for re-submission for Editor-only review. The authorship will be as follows; Lara A. Wood¹, Rachel L. Kendal² and Emma G. Flynn¹

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Abstract

This review investigates the presence of young children's model-based cultural transmission biases in social learning, arguing that such biases are adaptive and flexible. Section 1 offers five propositions regarding the presence and direction of model-based transmission biases in young children, claiming that such biases are adaptive. Section 2 discusses the cognitive abilities required for differing model-based biases and tracks their development in early childhood. Section 3 suggests some future areas of research including considering the social aspect of model-based biases and understanding their use within a comparative perspective.

Introduction

Social learning is ubiquitous in humans, and fundamental to children's development, but alone cannot explain the unique stability and diversity of human culture. Research into cultural evolution has escalated in recent years (Boyd, Richerson, & Henrich, 2011; Whiten, Hinde, Laland, & Stringer, 2011), increasing our understanding of the circumstances that facilitate social learning. Theoretical models of cultural evolution predict the evolution of flexible strategies enabling avoidance of unreliable or redundant information, and influencing the circumstances under which individuals copy others and from whom they learn (Boyd & Richerson, 1985). Thus, social learning is not seen as inherently adaptive and must be used selectively in the context of the environmental and model-based cues (characteristics of a demonstrator exhibiting a behaviour pattern) available to the observer. The use of such cues in guiding behaviour is known as 'cultural transmission biases' (Boyd & Richerson, 1985, also termed social learning strategies; Laland, 2004). Transmission biases refer to information, which has the potential to be socially learnt, being influenced by someone or something. Thus, a bias influences the likelihood of the social transmission of information. These are thought to increase fitness more than individual learning (Mesoudi & O'Brien, 2008) or unbiased social learning in which individuals acquire variants according to the frequency at which they are practiced (Rendell et al., 2011). This review discusses how the characteristics of models bias the likelihood that an observing child copies a model. Whilst focusing on instances of copying a model, we acknowledge that children are able to learn behaviour without necessarily reproducing every aspect of a demonstration (Bekkering, Wohlschläger, & Gattis, 2000; Flynn & Whiten, 2008; Williamson, Meltzoff, & Markman, 2008) and that copying a model may serve a function beyond simply

learning behaviours (Over & Carpenter, 2011). In Section 1, we argue that model-based biases enable children to gain the most useful information pertaining to their environment; hence a model-based bias is an *adaptive* cognitive tool that offers an evolutionary advantage. Throughout this review, adaptive means that the model-based bias contributes to an individual's survival by providing them with more useful behaviours within their environment than if such a model-based bias did not exist. In Section 2 we describe the developmental shift in the implementation of model-based biases, demonstrating increasingly flexible implementation. We conclude in Section 3 by discussing future considerations and directions.

Model-based Biases

As children develop they constantly witness alternative methods of achieving a goal. This has been mirrored in experiments where children witness divergent information from different models relating to tool-use (Wood, Kendal, & Flynn, in prep), and labels for elements in the environment (Koenig, Clément, & Harris, 2004). When faced with divergent information it would be adaptive to select and reproduce the information that achieves the outcome most suited for one's needs, but this can be complex. Models have different characteristics that influence our choice, including their previous performance, knowledge state, age, sex and social status. Furthermore, observers' own characteristics may influence who is the 'best' model for them. The potential list of relevant characteristics is endless and a naïve individual needs to evaluate these so that the behaviour of the most appropriate model, potentially providing the most useful and adaptive behaviour, is adopted.

It should be noted that, as mentioned above, social learning is not seen as universally adaptive. For example, social information might pertain to an outdated

environment. Social learning strategies are thought to increase the adaptive value of social learning. However, there may be instances whereby a model-based social learning strategy may not be inherently adaptive. For example, a bias towards copying a model that is successful in one domain might lead to other, non-adaptive behaviours, also being copied from this model. This "piggybacking" (Mesoudi & O'Brien, 2008, p 23) of non-adaptive behaviour from a particular model could lead to maladaptive behaviour. Whilst interesting, this review only focuses on cases where we expect a bias to result in adaptive social learning.

The adaptive value of model-based biases has been investigated in other fields, such as evolutionary biology, anthropology and non-developmental domains of psychology. Model-based biases have been described as 'who' biases (Laland, 2004), indirect biases (Boyd & Richerson, 1985) and context dependent model-based biases (Henrich & McElreath, 2003). Within developmental psychology it has long been established that it is important to understand whom children learn from, and that children's learning entails 'an active construct of the model by the individual' (Užgiris, 1981, p. 2). This review incorporates both evolutionary and developmental perspectives to argue that model-based biases are present, are adaptive, and are utilised more flexibly with ontogeny.

Section 1: The Adaptive Value of Model-based Biases

In this section we make five propositions regarding the adaptive value of model-based biases. To begin, we examine children's biases towards models whose behaviour indicates their desire to transfer information, namely children's receptiveness to pedagogical cueing. Second, we consider children's ability to evaluate and copy the most proficient individual before moving on to discussing

characteristics that identify models as belonging to groups with certain reputations that children may use to guide their learning. Fourth, we argue that the more similar a model is to a child, the more suitable s/he might be as a model, before finishing by discussing children's biases towards models that are prestigious.

Proposition 1: Children are Biased towards those who Intend to Teach

Csibra and Gergely (2009) argue that children have an innate predisposition for receptiveness towards people's ostensive signals indicating that the person is trying to communicate relevant information. These cues may include pointing, eye contact, and verbal directions. If a person is actively trying to communicate information then, generally, the person is communicating information about the environment that they believe will assist the observer. Being sensitive to a model's ostensive cues is adaptive because it enables children's attention to be drawn to important aspects of the environment. The sensitivity to ostensive cues is present from infancy, for example fourteen-month-olds search where they see someone point (Behne, Carpenter, & Tomasello, 2005). This sensitivity influences which models individuals copy; children imitate a model more when s/he stoops to the child's level, leans in, makes eye contact and talks engagingly (Brugger, Lariviere, Mumme, & Bushnell, 2007), gives verbal cues about the importance of actions (Southgate, Chevallier, & Csibra, 2009) or performs actions in a seemingly purposeful, rather than accidental manner (Carpenter, Akhta, & Tomasello, 1998; Gardiner, Greif, & Bjorklund, 2011). Indeed this receptiveness to pedagogical cueing is so strong it can limit exploratory play and discovery (Bonawitz, Shafto, Gweon, Goodman, Spelke, & Schulz, 2011). Thus children are receptive to pedagogical cueing and are biased towards copying models who attempt to share information about the environment.

Proposition 2: Children are Biased toward Copying the most Proficient Models

A model's success in a particular context indicates his or her ability to deal with that environment, therefore a successful model's behaviour is the most adaptive behaviour to adopt. There is evidence that infants are able to discriminate between models who act competently or incompetently (Zmyj, Buttelmann, Carpenter, & Daum, 2010) and seven-year-old children preferentially copy children rated by an experimenter as being competent rather than less competent (Brody & Stoneman, 1985). Likewise, the 'Trust' paradigm (Harris, 2007; Koenig & Harris, 2005a), whereby children are introduced to one reliable model (e.g., labels a ball, "ball") and one unreliable model (e.g., labels a ball, "shoe"), has demonstrated that, from infancy to six-years-old, children consistently copy reliable models over unreliable labellers for learning words (Koenig et al., 2004; Koenig & Harris, 2005b; Vázquez, Delisle, & Saylor, 2012) and artefact use (Birch, Vauthier, & Bloom, 2008; Zmyj et al., 2010). The labelling of artefacts from models who self-declare they know what is right (declaring, "this is a spoon") are more likely to be copied than models who are uncertain ("*I think* this is a fork"; Jaswal & Malone, 2007). Thus, children are able to discern the proficient model and are biased towards the information this model provides.

Proposition 3: Children are Biased toward Copying Models Belonging to a Group which has a Reputation for being Proficient

Employing model-based biases regarding an individual's proficiency is costly in terms of time and cognitive processing, as it requires an assessment of the behavioural history of a model. Instead, it is more efficient for an individual to be

biased towards characteristics of models that are easily identifiable, often indicating an individual's membership to a group. This group may have a different reputation for proficiency from another group leading to model-based biases. For example, a salient characteristic indicating group membership is age. A 'copy older over younger models' strategy seems adaptive because older individuals have had more experience with the environment and, by their continued existence, have made successful choices within the environment. Such age biases exist. Fifteen-month-olds are more likely to copy videotaped target acts when presented by an adult versus a two-year-old child (Seehagen & Herbert, 2011). Younger (one- to two-year-olds) siblings imitate the spontaneous social behaviours of their older (three- to five-year-old) siblings far more than the other way around regardless of age gap or sex differences (Abramovitch, Corter, & Pepler, 1980; Pepler, Abramovitch, & Corter, 1981). Three- and four-year-olds preferentially copy information provided by an adult over a child for novel word learning (Jaswal & Neely, 2006) and game rule learning (Rakoczy, Hamann, Warneken, & Tomasello, 2010), and seven- and eight-year-olds imitate the food choices of older rather than younger children (Brody & Stoneman, 1981). This bias towards learning from older individuals is also seen in the reproduction of causally irrelevant actions by children; when models use causally-inefficient tools, adults are more likely to be copied than children (Elekes & Kiraly, 2012), two- and three-year olds do not copy the irrelevant actions demonstrated by a peer to the same extent as when demonstrated by adult models (Flynn, 2008; Horner & Whiten, 2005), and three- and five-year-olds copy relevant actions of both child and adult models but only faithfully reproduce the irrelevant actions of adults (McGuigan, Makinson, & Whiten, 2011; Wood, Kendal, & Flynn, 2012). Potentially, children assume that increased age indicates increased proficiency

and use this bias to guide their learning (although see Section 2 for instances where this does not happen).

Proposition 4: Children are Biased toward Copying Models that Resemble Themselves

Individual differences result in individualised needs within an environment. These differences can influence children's proclivity to gain information from a model that is most similar to them, an 'observer-specific model-based bias'. This observer-specific bias may happen at a genetic, physiological or cultural level. For example, four- and five-year-olds generally accepted their mother's claims over those of a stranger (Corriveau et al., 2009) indicating that children may select information from those more genetically related to them. Familiarity is a confound to this interpretation, yet familiarity itself can be a marker of in-group membership and infants imitate more actions of a familiar, compared to an unfamiliar, model (Learmonth, Lamberth, & Rovee-Collier, 2005). Likewise, three- to five-year-old children, given conflicting artefact labels and functions from a known or unknown teacher, preferentially copy the known teacher (Corriveau & Harris, 2009b). Children also copy the choices of familiar models when choosing personal preferences or labelling artefacts (Shutts, Kinzler, McKee, & Spelke, 2009) and in tool use tasks (Buttelmann, Zmyj, Daum, & Carpenter, in press; Seehagen & Herbert, 2011). This preference for copying familiar models is adaptive because the child and the model have definite overlaps in their environment whereas the history of the stranger is unknown and, therefore, the information they provide may not be relevant for the child's particular environment.

Another salient physiological group difference is sex and whilst sex is not necessarily correlated to ability within our environment, children may be influenced by cultural sex-role norms. Indeed, eighteen-month-old children discriminate between stereotypical male and female artefacts (Serbin, Poulin-Dubois, Colburne, Sen, & Eichstedt, 2001). Likewise, three-year-olds copy the preferences of same-sex (over different-sex) child models for personal preferences of novel food, clothes, toys and games (Frazier, Gelman, Kaciroti, Russell, & Lumeng, 2011; Shutts, Banaji, & Spelke, 2010). This adoption of sex-specific behaviour may provide children with relevant information pertaining to their physiological needs or it may enable them to learn behaviours expected of their sex by their cultural group.

Learning other appropriate behaviours for one's cultural group seems fundamental to a child's development and there is evidence for a bias towards copying those belonging to the same cultural group. Twelve-month-old infants show a personal preference for foods endorsed by a speaker of their native language versus a model speaking a foreign language (Shutts et al., 2009). Likewise, Kinzler and colleagues found that five- and six-month-old infants attended more to a model speaking natural English over a model speaking 'reverse' English (the audio was played backwards) or a foreign language, and infants are also biased towards selecting a toy endorsed by a model speaking their native language (Kinzler, Corriveau, & Harris 2007) or using a native accent (Kinzler, Dupoux, & Spelke, 2011). Language is one of the most basic markers of cultural identity and, as seen with familiarity, a bias towards learning from models who share your culture may be adaptive because the cultural similarity indicates a shared environment, and, therefore, the behaviour of the most similar model may be the most relevant.

Proposition 5: Children are Biased towards Copying Models with High Status

Status incorporates two forms of social power; *dominance*, defined as an ability to acquire and monopolise resources over others, often through threatened or actual antagonism, and *prestige*, defined as status through non-agonistic means achieved through excelling in valued domains. Henrich and Gil-White (2001) note the importance of differentiating these two forms of status, which have their ‘own distinct psychology, selected for by distinct evolutionary pressures’ (p. 166). Humans can exhibit status through non-agonistic means and attainment of high prestige may reflect an individual’s superior ability to deal with his/her physical or social environment. The behaviour of high-status individuals, whether the status was acquired through skill or force, may thus be adaptive. In turn, it would be adaptive to copy models of high status, although such an adaption may result in copying behavioural traits that do not relate to the attainment of higher status (Mesoudi & O’Brien, 2008), hence the term ‘indirect bias’ (Boyd & Richerson, 1985).

Teacher ratings of social status and dominance of children correlate with observable characteristics, such as the age of a child (Grusec & Lytton, 1988), his/her size, and the number of wins in agonistic encounters with other children over resources (Pellegrini et al., 2007). Flynn and Whiten (2012) investigated both dominance and prestige in pre-school children’s social learning. There was evidence of a status-based model-based observation bias in these children; in a naturalistic, open diffusion setting with a novel puzzle-box, older children were watched more than younger children, popular children were watched more than less popular children, and more dominant children were watched more than less dominant children. This observation bias indicates a potential copying bias of more prestigious individuals. As dominant children did not monopolise the task, it seems they were

watched out of choice. Further, children were more likely to watch task manipulations made by peers they stated that they ‘liked’ rather than peers they stated that they did ‘not like’.

Whether a model is observed by others may, in itself, be a marker of prestige; four-year-old children use bystanders’ silent reactions to models such that a model who was ‘endorsed’ by bystanders through nods and smiles was copied more for labelling novel artefacts than a model whose behaviour was met with negative bystander reactions (Fusaro & Harris, 2008). This endorsement effect occurs even when the bystander attendance is neutral in comparison to an ignored model (Chudek, Heller, Birch, & Henrich, 2012). Children are receptive to the status of others and are biased towards learning from those who have higher status both in terms of dominance and prestige. It would be fruitful to explore the nature of the relation between model status and often associated characteristics, such as proficiency and age, to discover what factors contribute towards prestige. Likewise, to investigate whether biased copying from prestigious models is, in some circumstances, limited to behaviour which potentially contributes to the attainment of prestige, rather than being indiscriminate in this regard as theoretically assumed (Boyd & Richerson, 1985).

Summary

We have outlined five propositions relating to the presence and adaptive value of model-based biases. The evidence presented demonstrates that children monitor the characteristics or behaviour of others and use this to guide their own behaviour. Such abilities drive children to copy others, hence socially learn, in a discriminating manner. This behaviour goes beyond simply copying, as it is *biased*

copying and it is this bias which makes copying adaptive. The skills required for the implementation of biases are varied. Some model characteristics, such as a model's age and sex, are salient whilst others, such as proficiency and professed knowledge state, are more subtle. Evaluation of these more subtle cues requires the development of certain cognitive skills, such as an ability to track behaviour and understand the knowledge states of others. The next section presents some of the cognitive skills that improve the application of model-based biases and discusses their development in line with the findings from the social learning literature.

Section 2: The Development of Cognitive Skills Enabling Model-based Biases

This section reflects on some cognitive skills required in, infancy and early childhood which enable and assist in implementing model-based biases. The cognitive skills described here are relatively high-level and based on empirical papers detailing model-based biases. Therefore, lower-level cognitive processes such as working memory, categorisation or language development are not discussed, although future work addressing the influence of these processes on model-based biases seems pertinent. We argue that these cognitive skills enable children to flexibly employ model-based biases in response to environmental and behavioural cues. This flexibility is important because it allows children to move beyond the five propositions in Section 1 and continually source and copy the 'best' model.

From Infancy

Perspective taking. From infancy children respond differently depending on a model's visual access to stimuli and, therefore, potentially what the model knows (Koenig & Echols, 2003; Liszkowski, Carpenter, & Tomasello, 2008). This

perspective taking may facilitate the earliest forms of a model-based bias of proficiency. For example, a model who saw where a toy was hidden should be more proficient at locating the toy than a model who was unable to see where it was hidden. Such a proficient model is only more proficient in the immediate situation, as opposed to having a reputation for being proficient. In certain contexts (such as locating objects) this type of ‘immediate proficiency’ is more important than a reputation for proficiency; indeed, five-year-old children will rely more heavily on a model’s visual access (‘immediate proficiency’) than prior accuracy (‘reputation proficiency’) when locating a hidden object (Brosseau-Liard & Birch, 2011). This reflects flexibility in model-based bias use and whilst this research was conducted with five-year-olds, a consideration of context is seen from infancy.

Consideration of context. As seen above, the best model in one context may not be the best model in another context, and children appear to show flexibility in the model-based biases employed. Six-month-olds are more likely to copy an action demonstrated by their mother over a stranger (the experimenter) in the infants’ homes, but in a laboratory this pattern is reversed and they preferentially copy the experimenter (Seehagen & Herbert, 2012). These authors suggest that infants have expectations about the two models’ usefulness as teachers; they spend much time with their mothers who demonstrate pedagogical cues in the familiar environment. Conversely, an infant might have experienced unfamiliar people mostly in unfamiliar settings and, thus, have either formed the expectation that unfamiliar people are knowledgeable in unfamiliar environments or display associative learning of unfamiliar models in unfamiliar environments. Such appreciation of context is sophisticated and as these infants were only six-months-old it seems that adapting

model-based biases in different contexts is either automatic or learnt in the first few months of life and this flexibility may contribute to the biases adaptive value.

Context also affects biases toward copying models belonging to a particular group, such as an age group. One- and two-year-olds generally imitate spontaneous behaviour exhibited by adults more than peers, but the context affects this replication, such that imitation of parents is more likely to consist of motor skills (e.g. tool use) whereas affective behaviours are imitated from siblings and peers (Kuczynski, Zahn-Waxler, Radke-Yarrow, 1987). These two types of behaviour (motor skills and affective behaviours) represent different functions, and therefore could elicit different model-based biases. Indeed, four- to five-year-old children imitate adults more than children and same age peers when an action is novel, but copy a peer over an older child and adult when the action is not novel (Zmyj et al., 2011). In the first context, the function may be to learn a new skill and, therefore, children should be biased towards copying the model who they believe to be more knowledgeable (an adult over the child; Fitneva, 2010) whereas in the second context, the action is familiar and, therefore, the predominant motivation may be to learn behaviour appropriate to the child's own characteristics, i.e. learn what is appropriate for a child, and thus children copy the model who is most similar to them; another child. Indeed, when the context of the learning is play infants show higher fidelity copying of a three-year-old child versus an adult (Ryalls, Gul, & Ryalls, 2000) and peers over older children and adults (Zmyj, Aschersleben, Prinz, & Daum, 2012), and children also prefer clothes, toys, games and foods endorsed by children over those endorsed by adults (Shutts et al., 2010). Furthermore, in a diffusion chain paradigm, when an initial adult demonstrated functionally irrelevant actions, in a functionally oriented way, the first child copied these actions but

subsequent children parsed out the action of the child model they had witnessed (Flynn, 2008). Conversely, when an adult model demonstrated irrelevant actions in a playful way the behaviour spread; the children copied the child models (Nielsen, Cucchiaro, & Mohamedally, 2012). This implies children assess the context and copy individuals belonging to groups who will be most proficient in that context, so will most aid their learning, or adaptiveness to the environment. Alternatively and as touched upon in the introduction and discussed in Section 3, copying may not always be driven by a desire to learn but instead a desire to share a social experience (Užgiris, 1981), or become more integrated with a social group (Over & Carpenter, 2012).

Context also influences perceptions of the relative proficiency of one model (or group) over another model (or group). When three- to five-year-olds, presented with stick figure ‘adult’ or ‘child’ models, were asked who would provide more reliable answers to questions, children selected the adult when the questions were within the adult domain, such as the nutritional value of food, but when the subject area was toys children deferred to the child model (VanderBorghet & Jaswal, 2009). An ability to consider the domain of the behaviour alongside the model characteristics is adaptive as it allows for contextual flexibility in behaviour. Moreover, children demonstrate flexibility in their choice, such that when children are informed that a toy is ‘the adult’s favourite toy’ they defer to the adult, rather than a child model, for subsequent information regarding that toy (VanderBorghet & Jaswal, 2009). The additional flexibility of understanding that there may be exceptions to a domain appropriate model-based bias is cognitively sophisticated and adaptively biases the child towards the most proficient model in each specific instance.

Evaluating context may be the most important skill in ensuring that model-based biases towards certain models and categories (e.g. adult versus child) may be used flexibly. The flexibility of biases ensure that whilst children have biases towards learning from individuals based on their group membership they understand that these groups have different skills involving varying degrees of functional and social relevance for the observing child. Therefore, this flexibility increases the adaptive value of model-based biases.

Monitoring reactions to the model's behaviour. Context also involves monitoring the effect of a model's behaviour. This might be the physical effect of the action or, more subtly, it may relate to how others react to a model's behaviour. Infants are sensitive to the reactions of others and avoid imitating an action when unknown adults react negatively to an adult model actions (Repacholi, 2009) or show irritation towards the model (Repacholi & Meltzoff, 2007). A similar pattern is found in three- and four-year-olds when the model is a same-aged peer (Frazier et al., 2011) and also with novel word copying in four-year-olds who copy the novel artefact labels of models for whom bystanders react with smiles, more than the labels given by models for whom bystanders react with frowns (Fusaro & Harris, 2008). This ability to take account of the reactions of others could facilitate two model-based biases proposed in Section 1: first, the reactions of others may indicate that the model has performed a behaviour that pleases or displeases others and, therefore, indicates some degree of third-party evaluated model proficiency (proposition 2), and second, the reactions of others may be directed towards the model themselves and this could indicate some level of prestige (proposition 5). Presenting third-party bystanders who disapproved of clearly correctly modelled behaviour will help differentiate between

these biases. Either way, the ability to monitor the reactions of others is a useful skill in the implementation of model-based biases.

From early childhood

Evaluate the model's testimony. Evaluating model testimony is important for developing model-based biases pertaining to proposition 2 (children are biased toward copying the most proficient models) in the preceding section. Studies involving model testimony have shown that three-year-olds show mixed discrimination of proficient and less proficient models, with evidence of copying the behaviour of the reliable model (Birch et al., 2008; Corriveau & Harris, 2009a) but also a lack of discrimination of accurate over inaccurate informants (Koenig & Harris, 2005b). However, by four to six years, children consistently copy reliable models over unreliable labellers for learning words (Koenig et al., 2004; Koenig & Harris, 2005b; Vázquez et al., 2012) and artefact use (Birch et al., 2008). Six-year-olds also copy reliable labellers over tangential labellers, who are not inaccurate but fail to answer the question, although four-year-olds fail to make such a distinction (Vázquez et al., 2012). Furthermore, three-year-olds have difficulty discriminating between models when the reliable informant is anything other than 100% accurate, whereas four-year-olds are able to make distinctions between a model who was right 75% of the time versus a model who was right 25% of the time (Pasquini, Corriveau, Koenig, & Harris, 2007). Thus, with development comes an increasing ability to understand and evaluate a model's testimony, and hence develop increasingly sophisticated flexibility in the use of model-based biases regarding a model's proficiency.

Understanding knowledge states. Models can express different levels of confidence in their knowledge state by using terms such as ‘know’, ‘think’, ‘guess’ and ‘don’t know’ which present a scale of knowledge confidence. Children as young as three years are able to distinguish between a model verbally indicating uncertainty (“I think this is a spoon”) and one indicating certainty (“This is a spoon”) in a word learning paradigm (Jaswal & Malone, 2007), but struggle with subtleties of ‘know’, ‘think’ and ‘guess’ (Moore, Bryant, & Furrow, 1989). By four years, children are able to distinguish between ‘know’ versus ‘think’ or ‘guess’ and this improves with age, but until eight years children have difficulty distinguishing between ‘think’ and ‘guess’ (Moore et al., 1989).

Children also adapt to the context of the responses; if a model’s hesitant response could be caused by indecision rather than uncertainty, four-year-olds are more likely to accept a model’s artefact label (Sabbagh & Baldwin, 2001) so as children develop they become more skilled at evaluating the subtle differences in a model’s declared knowledge state. This understanding aids both children’s assessment of the potential proficiency of the model. For example, self-declared knowledge can assist in ascertaining the proficiency of the model. Model-based biases involving a model’s self-declared knowledge state occur from as young as three years of age, with increased word learning (Sabbagh & Baldwin, 2001; Sabbagh, Wdowiak, & Ottaway, 2003) and irrelevant action reproduction (Wood et al., 2012) following demonstrations from models with declared knowledge versus declared ignorance.

Assessing specialists and generalists. Humans have common shared knowledge; we all know the difference between cats and dogs. But we also have

specialist knowledge; doctors have expertise in anatomy while farmers have expertise with crops. It follows that if a model fails to show proficiency in shared general knowledge the perception of his/her proficiency should be more negatively affected than if the same model fails to show proficiency in an area of specialist knowledge. Young children are able to make this important distinction, as three- and four-year-olds do not copy a model who specialised in labelling dog species over a neutral model for novel artefact labelling, but a model who wrongly labelled dogs as cats was not chosen over a neutral model (Koenig & Jaswal, 2011). This skill improves with development (Koenig & Jaswal, 2011); whilst four-year-olds do not generalise beyond word knowledge having witnessed a reliable word labeller, five-year-old children generalise that the reliable word labeller will also excel in broader facts (Brosseau-Liard & Birch, 2010). This assessment of specialists and generalists allows children to use more subtle group membership model-based biases rather than more salient distinctions (e.g. age) whilst ensuring that they realise the potential limitations of this group membership.

Tracking prior personal experience and knowledge. Models do not always provide the best information available to a child. For model-based biases to be truly adaptive, children need to be able to not only compare one model with another, but should evaluate a model in comparison with their own knowledge and behaviour. This is evident in five-year-old children; when given no previous chance to interact with a task children will generally copy the irrelevant actions demonstrated by a model, but when they have successful prior interaction with a task, children will copy a new solution demonstrated by a model but parse out the causally irrelevant actions demonstrated by the model (Wood, Kendal & Flynn, 2013). Likewise, three-year-old

observers only use the false testimony of a model until their first failed attempt implementing this social information, and four- and five-year-olds improve upon this by only copying models up to the point at which the social information provided by the model conflicts with their personal information, the latter they then favour (Clément, Koenig, & Harris, 2004; Ma & Ganea, 2010).

As expected, a child's reliance on his/her personal information is affected by the interplay between the efficacy of his/her own behaviour and the efficacy of the model's actions, such that children with a difficult prior experience are more likely to imitate an adult's precise means of achieving something, compared to children with an easy prior experience (Williamson et al., 2008). When the choice of the model conflicts with the child's knowledge of an optimum tool for task completion, children ignore a model's choice unless the model explicitly states that her method is functionally appropriate or when the model's choice is only slightly less efficient than the child's preference (DiYanni & Kelemen, 2008). A developing confidence in one's personal knowledge within a task thus ensures effective evaluation of a model's behaviour, although over confidence in one's personal information causes the rejection of potentially useful social information (Jaswal, McKercher, & VanderBorgh, 2008). This relative assessment ability ensures that the model-based biases, whether they are towards models giving pedagogical cues, models with a reputation for proficiency or prestige, or models belonging to a group with a reputation for these characteristics, are not copied blindly. This ability to use prior information to critique behaviour ensures model-based biases represent adaptive heuristics.

Calibration of multiple pieces of information or cues. There are instances whereby children are presented with multiple pieces of information about a model and these may pertain to different biases as presented in Section 1. For example, a child may receive information from a proficient child or an incapable adult (Wood et al., 2012). When this occurs, children must calibrate biases regarding age and proficiency to guide their behaviour. For example, children favour older, over younger, children when making food choices, only until older models are shown to be less competent than younger models in an unrelated domain (Brody & Stoneman, 1985), and three- and four-year-olds will choose to label a novel object in accordance with a child model, rejecting the adult's label, if the adult's previous behaviour was unreliable (Jaswal & Neely, 2006). So, here children calibrate a group-based bias of model age against, the potentially more informative, proficiency bias and were more biased towards individual proficiency.

Such calibration also occurs with regard to familiarity and proficiency model-based biases. When three- to five-year-old children were given conflicting artefact labels and functions from a known or unknown teacher they copied the known teacher when no further information was provided (Corriveau & Harris, 2009b). However, when the unfamiliar teacher was more accurate than the familiar teacher at labelling familiar objects, four- and five-year-old children moderated their trust of the models, whilst three-year-olds showed little change in behaviour. Thus, development between three and five years demonstrates an emerging ability to calibrate across multiple model-based biases. There are a number of explanations for this; first, three-year-old children may have a model-based bias towards familiar adults but have not developed a proficiency model-based bias. Such an explanation is unlikely as from infancy children seem able to judge proficiency (Zmyj et al., 2010;

see proposition 2). Second, three-year-old children may be more influenced by the familiarity bias than a proficiency bias, perhaps due to a lack of social interactions with those who are unfamiliar. Third, three-year-old children may struggle with such calibration, perhaps due to a poorer working memory. Such a proposal could be tested by assessing the calibration of older individuals when a cognitive load is put upon their working memory.

There are other instances where children fail to calibrate; when two models *grasp* at opaque cups, three- to four-year-olds choose the cup grasped by the model who saw which cup held the reward (they choose the ‘seeing’ model), but when both models *point* at the different locations children did not favour the ‘seeing’ model, indicating that the pointing of the ‘unseeing’ model was confusing (Palmquist, Burns, & Jaswal, 2012). For children of this age, the model-based biases towards pedagogical cues (pointing) may be stronger than biases towards models that are proficient due to their visual access, the latter of which is more cognitively complex for the child’s understanding. Likewise, five-year-old children’s imitation of a model is more influenced by the model’s group membership (adult versus child) than the model’s knowledge state (model stating knowledge or ignorance about task completion) even though children of this age are able to correctly identify knowledge state (Wood et al., 2012). This indicates that a failure to correctly calibrate biases is not due to a lack of ability to implement one of the biases but due to the lack of experience a child has had with multiple biases or the cognitive load required within such calibration.

Alternatively, young children may understand that a model’s self-declared knowledge state is not always an accurate gauge of the reliability or utility of the behaviour they exhibit. A sophisticated assessment of a model’s credibility must

involve calibration of self-declared knowledge and behavioural accuracy of the model. Adults are able to make such calibrations (Tenney, MacCoun, Spellman, & Hastie, 2007; Tenney, Spellman, & MacCoun, 2008) but, whilst four- and five-year-olds are able to make accurate judgements regarding knowledge and accuracy independently, they are unable to discredit models that exhibit inconsistencies between knowledge and accuracy (Tenney, Small, Kondrad, Jaswal, & Spellman, 2011). This, again, supports the notion that children can process single model-based biases but find the calibration of multiple biases challenging. This section has demonstrated that there is a cognitive cost associated with model-based biases. Different types of model-based biases, such as a bias towards pedagogical cues, may be automatic and these may dominate in younger children until they are able to understand other biases, such as proficiency, and calibrate across these biases effectively.

Summary

We have highlighted some of the cognitive skills required for children to employ model-based biases. Many of these skills develop in the first five years of a child's life and are a vital part of a child's social cognition; for example, monitoring affect, perspective taking and language. Other cognitive skills enable children to move beyond employing model-based biases, to facilitating flexibility in their use; for example, understanding context, assessing specialists and generalists, tracking prior personal experience and calibrating multiple biases, abilities requiring other cognitive skills such as language and working memory. Additionally, children require experience, something that can only come with time. Flexibility in the use of

model-based biases is important as it allows children to move beyond simple biases to evaluating the context and the model's behaviour.

Section 3: Future Directions

We conclude this review by suggesting avenues of investigation of model-based biases beyond our argument of their adaptiveness and exploration of their development. Specifically, we focus on the emerging argument that social learning and, potentially, model-based biases are not solely based on individuals acquiring the best environmental information. We thus discuss and acknowledge the importance of the social interaction between the observer and the model. Following this, we highlight the usefulness of a comparative perspective, demonstrating that model-based biases in non-human animals show both convergences and divergences with that of children.

Understanding the Social Side of Model-based Biases

This review has deliberately focussed on the adaptive value of model-based biases, arguing that preferentially copying certain models will lead to learning the most adaptive behaviour for one's environment. However, we accept that we have assumed that the behaviours learnt are primarily functional (e.g. tool use or culturally appropriate). However, to-be learnt behaviour may also be inherently social, and social interaction is an additional or alternative function of imitation (Grusec, & Abramovitch, 1982; Over & Carpenter, 2012; Užgiris, 1981). Therefore, an interesting future direction would be to focus on the interplay between social and functional motivations to copy within the context of model-based biases. As seen in the previous section, discussing context, children's model-based biases change if the

to-be copied behaviour becomes more social (e.g. play) than functional (Zmyj et al., 2011). Investigating model-based biases in the context of how the content of the modelled behaviour affects the use of model-based biases would shed more light on whether the same biases are employed differently when the domain of the to-be-copied behaviour varies.

Additionally, it would be interesting to explore model-based biases which focus on the social behaviour of models, building upon work showing that how socially engaging a model is can affect whether children copy her or him (Elekes & Kiraly, 2012; Nielsen, 2006; Nielsen, Simcock, & Jenkins, 2008). Nielsen (2006) and Nielsen & Blank (2011) argue that this is due to a social motivation to share an experience or create an affiliation and that certain social, or indeed anti-social behaviours, influence the copying of functional behaviours. Furthermore, witnessing scenarios involving third-person ostracism can increase imitation in children (Over & Carpenter, 2009). This last example, whilst not demonstrating a model-based bias, does suggest that the model-based biases in the previous examples may be a by-product of an emotional reaction to a social situation rather than an evolutionary adaptation. Of course, such behaviour might be both an emotional reaction and adaptive, in that pro-social behaviour is thought to be an evolutionary adaptation (Dawkins, 1989). Thus children may be biased towards copying models that are pro-social both in order to obtain pro-social traits and because pro-social behaviour offers a degree of prestige.

Comparative Research

The adaptive nature of model-based biases has been discussed in relation to non-human animals' (henceforth animals) social learning (Laland, 2004). In the last

decade there has been a surge of activity directed at identifying and understanding the variety of biases that might influence social learning in animals (Kendal, Coolen, van Bergen, & Laland, 2005; Rendell et al., 2011). Work with animals demonstrates some interesting convergences with children. For example, in line with proposition 1 both dogs (Range, Viranyi, & Huber, 2007) and chimpanzees (Buttelmann, Carpenter, Call, & Tomasello, 2007), seem able to assess a model's intentions, and in line with proposition 2, some animals demonstrate biases toward the most proficient models, preferring to copy (sticklebacks, Duffy, Pike, & Laland, 2009) or observe (capuchins, Ottoni, de Resende, & Izar, 2005) the successful.

Regarding proposition 3, some animals are biased towards models belonging to a group that may have a reputation for being more proficient; stickleback fish copy the feeding location of older, larger fish as opposed to smaller, younger fish (Duffy et al., 2009). Mice are more influenced by the food choices of adult mice over younger mice (Choleris, Guo, Liu, Mainardi, & Valsecchi, 1997) and young female guppies copy the mate choice of older versus younger female guppies (Amlacher & Dugatkin, 2005). Wild chimpanzees show selective attention towards observing models of the same age or older, but not younger, than themselves (Biro et al., 2003), and captive chimpanzees' learning of food retrieval methods is influenced more by older versus younger individuals (Horner, Proctor, Bonnie, Whiten, & de Waal, 2010) and by dominant or 'expert' individuals (Kendal et al., in prep).

In line with proposition 4, some animals are biased towards models who are more genetically similar (rats; Saggerson & Honey, 2006) and more familiar (fish; Swaney, Kendal, Capon, Brown, & Laland, 2001) to themselves. With regard to proposition 5 some animals are biased towards individuals with high status; dominant individuals appear to elicit social learning more than subordinates in a

wide variety of species (e.g. chimpanzees, Bonnie, Horner, Whiten, & de Waal, 2007, Horner et al., 2010; capuchins, Dindo, Thierry, & Whiten, 2008; hens, Nicol & Pope, 1994, 1999; and seals, Sanvito, Galimberti, & Miller, 2007). However, the degree to which this is analogous to a copying high-status individuals bias in children depends upon the degree to which high-status represents aggressive force (power) or deference (prestige) in human and non-human species. Work with animals also offers some interesting interpretations for these biases. For example in lemurs, dominant individuals were more likely to be copied, as they monopolised resources (Kendal et al., 2010) and thus provided the most demonstrations (although this is not the case with the preferential observation of dominants in chimpanzees; Kendal et al. in prep.). In children non-monopolization of resources has been seen (Flynn & Whiten, 2012) yet the bias remained; the dominant children were watched out of choice. Another interesting interpretation from animal research is that increased social learning from a particular model may not always be due to model-based biases, but instead be due to an attentional by-product. Benskin, Mann and Lachlan (2002) and Katz and Lachlan (2003) suggest that female finches copy the feeding location of male rather than female conspecifics because females pay attention to males as potential mates, while females do not need to attend to one another. Conversely, male finches show no feeder preference because male finches pay equal attention to males (as potential rivals) and females (as potential mates). Likewise, male canaries are more innovative and better at personally learning a new feeding behaviour, but behaviours demonstrated by the females are more likely to be copied as the males are aggressive towards male observers (Cadieu, Fruchard, & Cadieu, 2010). Lastly, wild vervet monkeys learn to retrieve more food from an artificial fruit task when the task is modelled successfully by a female rather than a male, possibly because of females'

tolerance of observer presence (van de Waal, Renevey, Favre, & Bshary, 2010) or their likelihood, as the philopatric sex, of possessing relevant knowledge.

This body of work on animals suggests that model-based biases are not unique to humans. However, what may be unique to humans is the flexibility with which biases are used through children's developing ability to be receptive to pedagogical cues (Call & Tomasello, 1999), perspective take (Brosseau-Liard & Birch, 2011), categorise and generalise proficiency (Koenig & Jaswal, 2011), assess context (Zmyj et al., 2011) and calibrate multiple model-based biases (Jaswal & Neely, 2006), not to mention our species' understanding of complex language and higher-order mental state understanding (Jaswal & Malone, 2007). Alternatively, what could be unique to humans is that imitation serves a social as well as a functional motivation, as outlined above (Nielsen, 2009). Animals may have the ability to categorise and generalise proficiency, or calibrate multiple model-based biases, and these are avenues that need further investigation.

Conclusions

Children are prolific social learners, adopting the language, tool-use, knowledge and beliefs of those around them. We have highlighted that children do not source information indiscriminately, but rather use biases to guide their learning. What makes children's social learning truly impressive is their ability to implement strategies of model-based biases. These biases are adaptive in that they enable children to source the 'best' trait variant without the cost of assessing every trait variant displayed within the environment. Whilst some biases seem automatic, children need a suite of cognitive skills to use other model-based biases. These cognitive abilities are not all necessary for the occurrence of model-based biases, but

they all assist in ensuring model-based biases are effective, because they enhance children's appraisals of models and allow children to flexibly evaluate the context. Model-based biases and some of the accompanying cognitive skills required to learn and maintain these biases are not unique to humans. However, the combination of model-based biases and children's development of species-unique socio-cognitive skills (Dean, Kendal, Schapiro, Thierry, & Laland, 2012; Whiten & Erdal, 2012), such as language and understanding another's mental states, means that children stand alone in their ability to source the right model for them, in the right context, and use this model's behaviour to guide their own behaviour; resulting in a uniquely adaptive form of social learning.

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Chapter III

Context dependent model-based biases in cultural transmission: Children's imitation is affected by model age over model knowledge state.

This chapter is an empirical study investigating children's model-based biases relating to two characteristics. Specifically, the age and stated knowledge state of a model were manipulated to investigate the fidelity of children's copying. This chapter is published, as is, in *Evolution and Human Behavior*, (2012) 33(4), 387-394.

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Abstract

Many animals, including humans, acquire information through social learning. Although such information can be acquired easily, its potential unreliability means it should not be used indiscriminately. Cultural ‘transmission biases’ may allow individuals to weigh their reliance on social information according to a model’s characteristics. In one of the first studies to juxtapose two model-based biases, we investigated whether the age and knowledge state of a model affected the fidelity of children’s copying. Eighty-five 5-year-old children watched a video demonstration of either an adult or child, who had professed either knowledge or ignorance regarding a tool-use task, extract a reward from that task using both causally relevant and irrelevant actions. Relevant actions were imitated faithfully by children regardless of the model’s characteristics, but children who observed an adult reproduced more irrelevant actions than those who observed a child. The professed knowledge state of the model showed a weaker effect on imitation of irrelevant actions. Overall, children favoured the use of a ‘copy adults’ bias over a ‘copy task-knowledgeable individual’ bias, even though the latter could potentially have provided more reliable information. The use of such social learning strategies has significant implications for understanding the phenomenon of imitation of irrelevant actions (overimitation), instances of maladaptive information cascades and for understanding cumulative culture.

Introduction

The adaptive value of social learning is now evident in a vast range of animals, from humans to insects, increasing our understanding of cultural evolution and social intelligence (Boyd & Richerson, 1985; Tennie et al., 2009; Whiten & van Schaik, 2007). When acquiring information individuals face evolutionary trade-offs between the acquisition of costly but accurate personal information and the use of cheap but potentially less reliable social information (Boyd & Richerson, 1985; Kendal et al., 2005). Accordingly, the use of social information should be determined by an evaluation of the content of the information presented and the characteristics of the information provider, the model (e.g. Henrich & Gil-White, 2000; Rendell et al., 2011; van Bergen et al., 2004). Nevertheless, the transmission of information from one individual to another has resulted in the accumulation of errors or cascades of misinformation (Rieucou & Giraldeau, 2009; Tanaka et al., 2009). For example, humans copy non-functional attributes (Mesoudi & O'Brien, 2008), and maladaptive behaviors pass between individuals within groups (McGuigan & Graham, 2009; Whiten & Flynn, 2010).

Furthermore, humans copy actions that, at face value, appear to be causally irrelevant to their goal (Horner & Whiten, 2005). The propensity to copy these irrelevant actions appears in different cultures (Nielsen & Tomaselli, 2010), increases with age (McGuigan et al., 2007; Nielsen, 2006) into adulthood (McGuigan et al., 2011), and persists despite interventions such as reinforcement for the identification of irrelevant actions and direct instructions to only copy relevant actions (Lyons et al., 2007, 2011). Such pervasiveness has led some to view copying irrelevant actions as, 'an evolutionary adaption that is fundamental to the development and transmission of human culture' (Nielsen & Tomaselli, 2010, p.729). For example, imitating apparently

causally irrelevant elements of tool use demonstrations may help children acquire means actions before they fully understand their causal role (Hernik & Csibra, 2009). If one does not know whether an action is causally necessary it may be adaptive to copy this action.

Copying causally irrelevant actions could only be adaptive if individuals develop flexible strategies that dictate the circumstances under which they copy others. Theoretical models have explicitly considered heuristics that may be adopted in social learning, which have been termed ‘social learning strategies’ (Laland, 2004) and ‘cultural transmission biases’ (Boyd & Richerson, 1985; Rendell et al., 2011). According to Boyd and Richerson (1985), individuals may employ an *indirect* bias towards learning from a model with specific preferential characteristics. These indirect biases, or *context-dependent* (Henrich & McElreath, 2003) model-based biases, include characteristics such as the model’s age. Using such model-based biases allows populations to approach adaptive optima much faster than they otherwise would under individual learning or ‘guided variation’ (Boyd & Richerson, 1985). For example, Mesoudi and O’Brien (2008) found, by simulating the cultural transmission of prehistoric projectile-points, that the population-level pattern observed in Nevada’s archaeological record was consistent with a bias of *wholesale* copying of a successful hunter’s projectile-point design, including non-functional but selectively neutral aspects (such as color), rather than copying particular projectile-point attributes.

In an argument analogous to that of Laland (2004) regarding the relative abundance of cognitively challenging versus simpler social learning strategies in the animal kingdom, we argue that within a species there may be differences in the propensity to use certain model-based biases. Specifically, children may find a ‘copy adult over child’ strategy relatively easy to implement compared to a ‘copy task-

knowledgeable individual' strategy (Henrich & Broesch, 2011) for a number of reasons. First, an understanding of age develops earlier than an understanding of knowledge (Edwards, 1984; Wellman et al., 2001) and thus related biases may also develop earlier. Second, age may be a more salient characteristic and thus involve less cognitive processing. Third, children may understand that self-declared knowledge states may be less reliable than age. In the current study five-year-old children received demonstrations of observably relevant and irrelevant actions in relation to the goal of extracting a reward from an artificial fruit and we investigated whether the observing child's subsequent behavior was influenced by the model's age and/or knowledge state.

Kirkpatrick and Dugatkin (1994) found the strategy of 'copy older individuals' to be a prominent heuristic. There is evidence that older models elicit more social learning than younger models in many species (e.g. seals, Sanvito et al., 2007; mice, Choleris et al., 1997; guppies, Amlacher & Dugatkin 2005, Dugatkin & Godin, 1993; chimpanzees, Biro et al., 2003, Horner et al., 2010). Likewise, human developmental research has considered model age as a determining factor in social learning for some time. Observational studies have shown that younger (1- to 2-year-old) siblings imitated their older (3- to 5-year-old) siblings far more than the other way around regardless of age gap or sex differences (Abramovitch et al., 1980; Pepler et al., 1981). When presented with two models of differing ages (two years younger, same age, or two years older) simultaneously, eight year olds imitate the food preference choice of older and same age peers over younger peers (Brody & Stoneham, 1981). Similarly, when the two models presented were a child and an adult, three- and four-year-olds preferentially used information provided by an adult over a child, for word learning (Jaswal & Neely, 2006) and simple rule games, interpreting the adult's behavior as normative (Rakoczy et al., 2010)

The effect of a model's age on children's social learning is modulated by the content of the to-be-copied behavior. Two-action, artificial fruits tasks have shown that 14-month-old infants (Hanna & Meltzoff, 1993) and 3-, 4- and 5-year-old children, (Flynn & Whiten, 2008a; Hopper et al., 2008, 2010) imitate relevant actions performed by a peer to the same extent as children in studies with adult models (McGuigan et al., 2007). However, studies looking at the imitation of irrelevant actions show that 2- and 3-year old children did not copy the irrelevant actions demonstrated by a peer to the same extent as irrelevant actions presented by an adult model (Flynn, 2008; Horner & Whiten, 2005). Subsequently, McGuigan et al. (2011) explicitly investigated the effect of a model's age on the copying of irrelevant actions. Observers of various ages (3- and 5-year-olds and adults) copied significantly more irrelevant actions when they were modelled by an adult as opposed to a 5-year-old child. It remains unclear whether this disposition indicates a bias of 'copy adults' or the more cognitively complex bias of viewing a child model as 'less rational and knowledgeable' than an adult model (Flynn 2008, p. 3549).

The effect of a model's knowledge state on children's social learning strategies is less clear. By five years of age children have a concept of a model's expertise (Azmitia, 1988; Birch et al., 2008, 2010; Moore et al., 1989), knowledge (Koenig & Harris, 2005; Sabbagh & Baldwin, 2001; Wellman et al., 2001), intention to teach (Ziv et al., 2008) and infer a model's knowledge state based on his/her age (Taylor et al., 1991). One might expect observers to rely more heavily on an individual's demonstration when that individual has professed knowledge in the specific task domain (Henrich & Broesch, 2011). Furthermore, although there has been theoretical speculation of the existence of a hierarchy of transmission biases (McElreath et al., 2008), the interaction between biases remains unclear. We are only aware of one study

investigating the interaction of copying biases of children of a model's age and competence. In this study the competence information, exhibited in an unrelated task, outweighed age information such that children (aged 7- to 8-years-old), in order of preference, copied: a high-competence peer, a high-competence younger model, a low-competence peer and low-competence younger model (Brody & Stoneman, 1985). To test a task-directed context bias, however, one must manipulate the model's professed knowledge state of the specific task.

The current study explicitly investigated the effect of two model-based biases on children's copying fidelity. We contrasted the model's age (adult versus peer model) with a bias that might require greater assessment, the model's task-directed knowledge state (task-knowledgeable versus task-ignorant model). The completion of a two-action tool-use task (Dawson & Foss, 1965), which included causally relevant and irrelevant components, was demonstrated by one of four models differing with respect to these biases. We predicted that: (1) an observer who witnessed a model successfully extract a reward from a task would imitate the relevant actions demonstrated using the same means to extract the reward regardless of the model's characteristics. (2) In line with McGuigan et al. (2011), children who witnessed an adult model would exhibit higher levels of imitation of causally irrelevant actions than those who witnessed a child model. (3) Children faced with a task-knowledgeable model would show higher levels of imitation of causally irrelevant actions than those presented with a task-ignorant model. Finally, (4) in line with Brody & Stoneman (1985), there would be a hierarchy of transmission biases with a task-knowledgeable adult facilitating the highest level of imitation of irrelevant actions, and a task-ignorant child producing the lowest levels of imitation of irrelevant actions, with potential differences between the two other models allowing the hierarchy of biases to be examined further.

Method

Participants

Ninety-six 5-year-old children (45 males, $M = 65$ months, $SD = 3.5$ months) from schools in County Durham participated. There were no significant differences for sex, [$\chi^2(8, N = 96) = 2.29, p = .97$] or age ($F_{8, 87} = 0.81, p = .60$) across the experimental conditions and the no model control.

Materials

A two-action task, the transparent version of the ‘Glass Ceiling Box’ (GCB; see Figure 1, Flynn, 2008; Horner & Whiten, 2005; McGuigan & Graham, 2009; McGuigan et al., 2007; 2011) was used. The GCB is a transparent box with an opening at the front that can be revealed by sliding or lifting a door. The goal is to retrieve a Velcro-backed sticker reward from a tube located behind the door, by inserting a stick tool (a 22cm rod with Velcro on the end) into the tube. The demonstrated actions directed to the door at the front of the GCB are causally necessary to retrieve the reward. The GCB has a further opening in the roof, covered by a two-bolt defence that can be removed by poking or dragging them from the opening with the stick tool. This hole leads to an empty compartment with a ‘glass ceiling’ preventing physical access to the reward, so actions directed to the bolts or the upper compartment are observably causally irrelevant to retrieving the reward.

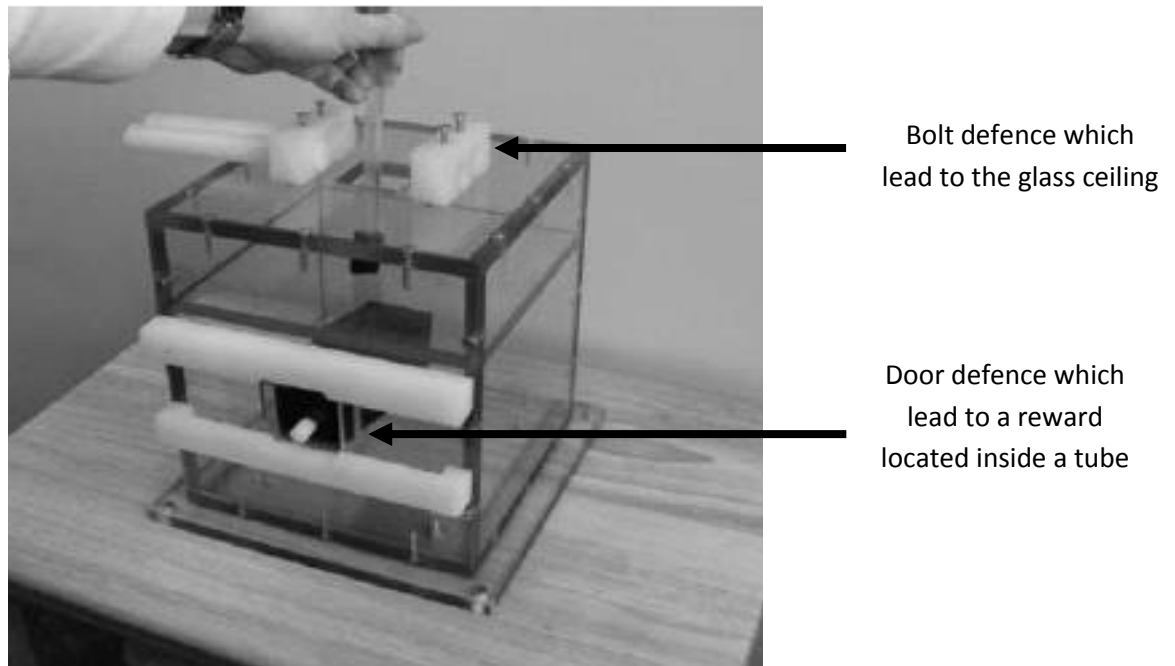


Figure 1. The Glass Ceiling Box (GCB) showing a model performing one of the irrelevant actions. Photo from Flynn (2008).

Design

A between-groups design was used, with children randomly allocated to one of four conditions pertaining to the model's characteristics (adult professing knowledge, adult professing ignorance, 5-year-old professing knowledge and 5-year-old professing ignorance, $N = 85$) or a no model control ($N = 11$). The control group was relatively small as the GCB has been administered in several experiments (Flynn, 2008; Horner & Whiten, 2005; McGuigan et al., 2007, 2011) with controls showing similar levels of interaction and success as shown in the current experiment. Both models were female and unknown to the participants. After observing a video of the model's initial entrance and profession of knowledge or ignorance about task completion, participants watched one of two video demonstrations of the reward being extracted from the GCB. These clips were identical, regardless of the model's age, and counterbalanced across

conditions; the only difference was the depiction of different methods (method 1, poke-bolts-then-slide-door, and method 2, drag-bolts-then-lift-door). As participants had more than one response trial, there was a within-groups variable of trial number (T1 and T2). In the no-model control condition children were presented with the GCB without witnessing any demonstration.

Procedure

Children were tested individually in a quiet place in their school. Each child sat at a table in front of a laptop computer with the GCB on an adjoining table. The child was told, “Today I have brought in this toy. This is a video of me showing the toy to Emma. Watch closely and listen carefully.” The child then watched an introduction to one of the video demonstrations in which the model walked into a room, looked at the GCB and turned to the camera professing either knowledge, “I know this game, I’ve played with it lots of times, I know exactly how to do this” or ignorance, “This is a new game, I have never seen it before, I don’t know how to do it.” Children watched this introduction twice and after each viewing were asked, “Had Emma seen the game before? Did she know how to do it?” By the second viewing all participants answered correctly.

Then the child was told, “We asked Emma to play with the box and recorded what happened.” Children watched one of two video demonstrations of either the method 1 or method 2 sequences of actions being carried out on the GCB. Unlike McGuigan et al. (2011), these video clips showed only the hands and arms of a petite adult. Thus any difference in participant’s behavior was due to model characteristics alone and not the physical differences in the demonstration (e.g. motor coordination) or ostensive cues. Twenty adults, blind to the study, watched the video clips and were

asked who performed the actions. All labelled the demonstrations as desired, with those seeing a child at the beginning labelling the demonstration as having been performed by a child and those who witnessed an adult at the beginning attributing the actions to an adult.

The sequence of actions was as follows: the tool was used to remove *two* bolts on top of the GCB either by poking or dragging, the tool was inserted into the top hole and the glass ceiling tapped *three* times (totalling five irrelevant actions), a door at the front of the GCB was moved by either sliding or lifting it, the tool was inserted and a sticker removed. Children watched the video demonstration of the sequence of actions twice and were then told, “I would like you to play with the toy. There is no right or wrong way. I just want to see you play.” The child was allowed to interact with the GCB (T1) until (s)he retrieved the reward successfully or three minutes had elapsed. If required, children were given a prompt, “You can play with it as much as you like.” Each child was then shown the demonstration clip a third time and allowed a further attempt (T2).

In the no-model condition each child was told, “Lots of children have played with this toy today and now I would like you to play with it.” They received three minutes with the GCB and were given the same prompt as the experimental group. All children were rewarded with a sticker for their participation, regardless of their success.

Analysis

Each participant’s performance was scored on four variables, i) successful removal of the sticker, ii) method used to open the door iii) method used to remove the bolts and, iv) how many irrelevant actions were copied. The experimenter coded all children’s behavior whilst two independent observers, blind to the children’s allocated

condition, coded 26% of the sample. All Cronbach's Alpha scores were 0.95 or above, showing an excellent level of rater-reliability.

Results

All of the dependent variables (i to iv above) were compared between conditions (type of model) and within participants (T1 versus T2). Children who observed a demonstration were significantly more successful at retrieving the reward at T1 (success rate = 68%, $p < .01$ Fishers Exact Test, one tailed) than children in the control condition (18%), with a significant increase in success from T1 to T2 (McNemar $Z_{1, 85} = -3.21$, $p < .01$).

Copying of Causally Relevant Actions

No child in the no-model control condition lifted the door, while ten slid it. The number of children in the experimental conditions who copied the door-opening method they witnessed was significantly greater than chance with 71% copying the method at T1 [$\chi^2(1, N = 68) = 11.53$, $p < .001$] and 72% at T2 [$\chi^2(1, N = 74) = 13.84$, $p < .001$]. Our first hypothesis was that model characteristics would not affect the copying of causally relevant actions. To test this we ran a multi-level logistic regression of relevant actions across T1 and T2 with corrected standard errors to account for the dependence between a child's T1 and T2 behavior. Model age, model knowledge state and demonstration witnessed (slide or lift) were entered as predictors and copying of action witnessed was the dependent variable. Age and knowledge state were not significant predictors of the imitation of the relevant actions. The demonstration witnessed (lift or slide) was a significant predictor (see Table 1), children copied the door-slide method more than the door-lift method (97% slide, 46% lift).

Table 1. The effects of a model's age and knowledge state and demonstration witnessed on relevant actions copied. Logistic regression with standard errors

| Parameters | Estimate (SE) | |
|------------------------------------|---------------|----------------------|
| Intercept | 1.74 | (0.47) *** |
| Model Age ^a | 0.35 | (0.44) ^{ns} |
| Model Knowledge State ^b | 0.46 | (0.44) ^{ns} |
| Demonstration ^c | 1.76 | (0.44) *** |

^a Dichotomous variable 0=child 1=adult; ^b Dichotomous variable 0= ignorant

1=knowledgeable; ^c Dichotomous variable 0=lift 1=slide; ^{ns} $p > .05$, *** $p < .001$ (two tailed).

Copying of Causally Irrelevant Actions

Only two children in the control condition produced an action directed to the (causally irrelevant) bolts, both poking them, and no child tapped the tool into the upper compartment. Baseline behavior comparisons were made between the children in the control group and the experimental children at T1 only, as by T2 the children had experience with the GCB. Children who observed a demonstration performed significantly more irrelevant actions at T1 ($M = 1.55$, $SD = 1.74$, $t_{34} = -4.72$, $p < .001$.) than control children ($M = 0.27$, $SD = 0.65$). In the experimental conditions, the number of children who copied the bolt removal method they witnessed was significantly greater than chance at T1 [$\chi^2(1, N = 48) = 16.33$, $p < .001$] and T2 [$\chi^2(1, N = 60) = 23.67$, $p < .001$]. As the bolt method witnessed did not affect the total number of irrelevant actions performed at T1 ($t_{83} = -1.54$, $p = .13$) or T2 ($t_{83} = -1.61$, $p = .11$), the data were collapsed across methods.

It was hypothesised that children would imitate more irrelevant actions when they were presented by an adult as opposed to a child and when presented by a self-

reported knowledgeable model as opposed to an ignorant model. To test this we conducted a Poisson regression analysis of irrelevant actions, using joint modelling with robust standard errors to account for the dependence between a child's T1 and T2 behavior, with model age, model knowledge state, participant age and participant sex entered as predictors. Participant age and sex were not significant predictors. As expected, model age was a significant predictor (adult model, $M = 2.26$, $SD = 1.81$, child model $M = 1.51$, $SD = 1.80$, $p < .05$), but, contrary to expectation, knowledge state was not (see Table 2 and Figure 2). Thus, whilst children who witnessed an ignorant model produced fewer ($M = 1.71$, $SD = 1.78$) irrelevant actions than children who witnessed a knowledgeable model ($M = 2.05$, $SD = 1.89$, $p = .18$), this difference was not significant.

Table 2. Effects of a model's age and knowledge state and participant demographics on the number of irrelevant actions performed. Poisson regression using joint modelling with robust standard errors

| Parameters | Estimate | (SE) |
|------------------------------------|----------|----------------------|
| Intercept | 0.55 | (1.75) ^{ns} |
| Trial 2 – Trial 1 | 0.35 | (0.01) *** |
| Model Age ^a | 0.41 | (0.18) * |
| Model Knowledge State ^b | 0.24 | (0.18) ^{ns} |
| Participant's Sex ^c | 0.24 | (0.18) ^{ns} |
| Participant's Age | -0.01 | (0.03) ^{ns} |

^a Dichotomous variable 0=child 1=adult; ^b Dichotomous variable 0= ignorant

1=knowledgeable ; ^c Dichotomous variable 0=male 1=female; ^d Continuous variable

age (months); ^{ns} $p > .05$, * $p < .05$ (two tailed), *** $p < .001$ (two tailed).

Pairwise comparisons of the four conditions (knowledgeable adult, knowledgeable child, ignorant adult, ignorant child) showed that, whilst children presented with the child-ignorant model performed significantly fewer irrelevant actions compared to children presented with the adult-knowledgeable model ($t_{78} = 2.66, p < .01$), no other differences were significant (see Figure 2).

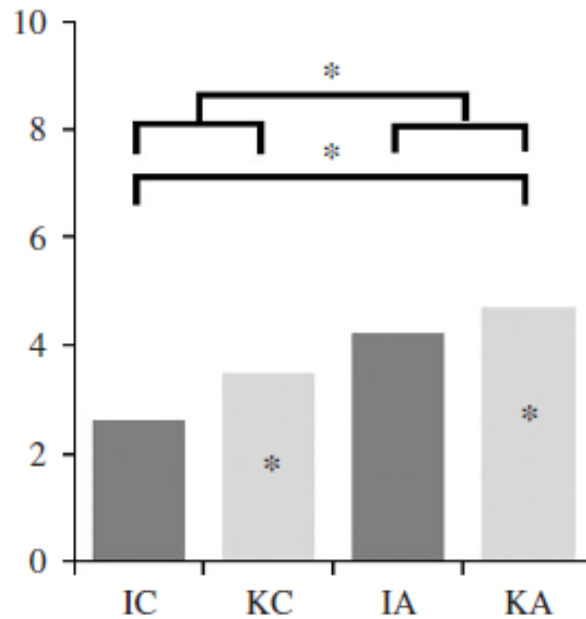


Figure 2. Mean number of irrelevant actions (out of 10) performed depending on model identity over the two trials.

Note. IC: ignorant child, KC: knowledgeable child, IA: ignorant adult, KA: knowledgeable adult. Asterisks indicate a difference in means more than expected between groups ($*p < .05$). Asterisk within a bar indicates a significant increase in irrelevant actions from T1 to T2 ($*p < .05$).

Post-hoc Analysis

Overall, children produced significantly more irrelevant actions at T2 ($M = 2.21$, $SD = 1.89$) than T1 ($M = 1.55$, $SD = 1.74$; $t_{84} = -3.71, p < .001$). This increase was significant for those who observed a knowledgeable adult (paired t-test: $t_{19} = -2.53, p < .05$).

.05, Cohen's $d = 0.56$), and a knowledgeable child ($t_{22} = -2.08$, $p < .05$, $d = 0.40$) but not for those who observed an ignorant adult ($t_{21} = -1.87$, $p = .08$, $d = 0.28$), or an ignorant child ($t_{19} = -0.98$, $p = .34$, $d = 0.28$, see Figure 2), although the power for the latter two tests was low.

Discussion

The current study extends research into cultural transmission by explicitly examining the role of, and relation between, two different model-based context dependent transmission biases: age and professed task-knowledge state. The results confirmed two of our initial predictions, (1) that children would imitate relevant actions regardless of a model's age and knowledge state, and (2) that children would imitate more causally irrelevant actions produced by an adult than a peer. Our third and fourth predictions, (3) that children would use a task-directed bias to imitate irrelevant actions produced by a task-knowledgeable, but not task-ignorant, model and (4) that there would be a hierarchy of transmission biases, received comparatively weaker support.

As predicted, and in line with previous findings (Flynn, 2008; Flynn & Whiten 2008a, 2008b; Hopper, et al., 2008, 2010), the model's characteristics did not affect the high levels of imitation of the relevant actions. Such faithful imitation of relevant actions appears to be canalisation, where the various possibilities for manipulating a task are reduced after a social demonstration (Flynn & Whiten, 2008a; Hopper et al., 2010; Horner, et al., 2006). This is clearly illustrated by the 46% of children who observed the door of the GCB being lifted and produced a lift action despite the availability of a preferred more salient slide method.

We posit that young children exhibit a social learning strategy (Laland, 2004) of '*faithfully* copy adults' because, whilst children copied relevant actions from both peers

and adults, they copied significantly more irrelevant actions when demonstrated by an adult versus a peer. The demonstrations were presented on video, and all children witnessed the same pair of hands manipulating the task, regardless of condition, so the bias we witness for children to copy an adult over a peer was not due to any ostensive cues present in the demonstration. Such a finding is in line with McGuigan et al. (2011), who found similar results with three- and five-year-old children. The irrelevant actions in the current study were not neutral (Mesoudi & O'Brien, 2008) but entailed a cost in terms of delaying reward acquisition. This demonstrates the potential power of such transmission biases to establish maladaptive information cascades, sometimes at the population level (Bikhchandani et al., 1998; Henrich & McElreath, 2003).

A task-directed bias of 'copy task-knowledgeable individuals' did not override the tendency to copy adults, despite the fact that the children in the current study could correctly identify the model's knowledge state. In contrast, when Brody & Stoneman, (1985) juxtaposed peer age and competence (on an unrelated task), a competence bias outweighed any age bias, such that younger peer/high-competence models were preferred over same-age peers/low competence ones. Whether this difference in results is due to the model's ages (adult and child model versus younger and same age peer model), reputation (knowledge state versus reliability) or medium of competency (self-declared in a video clip versus a description given by an adult experimenter) are unclear but is ripe for further exploration.

Whilst the regression model of irrelevant actions indicated that knowledge state was not a significant predictor, pairwise comparisons (of the four model types) showed that a knowledgeable adult demonstration resulted in more irrelevant actions being produced than an ignorant child demonstration; no other groups differed significantly. Thus a model's age was weighted over the professed task-knowledge, but task-

knowledge was evaluated to some degree, lending some support to the idea that there is a hierarchy of transmission biases as reported by McElreath et al. (2008). Additionally, post hoc analysis revealed that children, who witnessed knowledgeable models, reproduced significantly more irrelevant actions at their second attempt than children witnessing ignorant models, who showed no change across their attempts. Taken together these results provide limited support for a knowledge-based strategy.

Our findings provide, to our knowledge, the first evidence in any species (consistent with the analogous prediction of Laland, 2004) that, in decisions pertaining to the cultural transmission of information, easily adopted heuristics, such as age-based biases, may be more readily used than more cognitively challenging biases, such as those involving assessment of another's knowledge state with regard to the task at hand. The question then is, whether an age bias is inherently more adaptive than a knowledge state bias or whether it is simply easier to evaluate? Whilst there is an argument that children may understand that self-declared knowledge states may be less reliable than age, we believe it is more likely that the preference for a 'copy adult over child' strategy involves less cognitive processing and is a by-product of its relative ease to implement. An understanding of age develops earlier than an understanding of knowledge (Edwards, 1984; Wellman et al., 2001) and thus related biases may also develop earlier.

This cognitively easier assessment of a model's age may, however in itself, be adaptive because adults, by their increased experience with the world, are generally more proficient and knowledgeable models than children. Children infer a model's knowledge state based on his/her age (Taylor et al., 1991), thus this correlation may lead to effective social learning strategies. However, when the correlation is contradicted, and there are instances of ignorant adults or knowledgeable children, children still rely on the age bias, resulting in the current study's finding that children

are as likely to copy the irrelevant actions of an ignorant adult as a knowledgeable child. This occurred even though every child was able to correctly identify the knowledge state of the model. Thus, it would be informative to conduct future research into children's developing ideas of the inter-relation between age and knowledge state.

The relation between these biases also helps us to understand the phenomenon of copying causally irrelevant actions. The children's selective reproduction of causally irrelevant actions suggests that this phenomenon may not be as pervasive as previously thought (Lyons et al., 2007; Nielsen & Tomaselli, 2010) in that the replication of irrelevant actions was modulated in response to a model's characteristics. However, that is not to say that imitation of irrelevant actions can no longer be considered an evolutionary adaptation (Nielsen & Tomaselli, 2010). The copying of causally irrelevant actions may reflect a cognitively complex process within a child, involving assumptions about the 'irrelevance' of particular actions. For example, it would be adaptive for children to evaluate which seemingly causally irrelevant actions may be relevant actions whose causal efficacy they are yet to understand (Hernik & Csibra, 2009) versus those actions which are simply irrelevant. A wise assumption may be that adults are more likely to produce 'irrelevant' actions that actually have an opaque function of social or cultural relevance, whilst irrelevant actions of peer-aged children should be taken at face value. Therefore an overriding strategy of 'adults should be imitated faithfully, children should be imitated unless their actions seem non-functional' may be extremely adaptive, even though this heuristic may sometimes lead to the copying of irrelevant actions.

High fidelity copying is a necessary factor underlying the unique capacity of humans for cumulative cultural transmission (Boyd & Richerson, 1985). Faithful imitation is the bedrock of cultural ratcheting (Tennie et al., 2009) as it prevents any

loss of knowledge, allowing for potential improvement in subsequent individual development and/or generations. Faithful imitation of causally irrelevant actions, as exhibited in this study, may appear to conflict with our species' capacity for cumulative culture due to its potential to lead to cascades of misinformation. However, the current study has demonstrated that the selective nature of children's social learning, in copying adults over children and potentially assessing the irrelevance of apparently causally irrelevant actions, explains why a more likely result is the advancement of complex, socially learned behaviours.

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Chapter IV

Copy me or copy you?

The effect of prior experience on social learning

The previous chapter (Chapter III) revealed that continued demonstration and interaction affected imitation of irrelevant actions relative to model identity such that those who witnessed a knowledgeable model increased the number of irrelevant actions they performed more than those who witnessed an ignorant model. This task behaviour change is explicitly tested in Chapter IV, an empirical study investigating children's solution choice and social learning mechanisms following differing prior experiences and multiple social demonstrations. This chapter is published, as is, in *Cognition*, (2013), 127(2), 203-213.

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Abstract

The current study investigated children's solution choice and imitation of causally-irrelevant actions by using a controlled design to mirror naturalistic learning contexts in which children receive social information for tasks about which they have some degree of prior knowledge. Five-year-old children ($N = 167$) were presented with a reward retrieval task and either given a social demonstration of a solution or no information, thus potentially acquiring a solution through personal exploration. Fifty-three children who acquired a solution either socially or asocially were then presented with an alternative solution that included irrelevant actions. Rather than remaining polarised to their initial solution like non-human animals, these children attempted the newly presented solution, incorporating both solutions into their repertoire. Such an adaptive and flexible learning strategy could increase task knowledge, provide generalizable knowledge in our tool-abundant culture and facilitate cumulative culture. Furthermore, children who acquired a solution through personally acquired information omitted subsequently demonstrated irrelevant actions to a greater extent than did children with prior social information. However, as some children with successful personally acquired information did copy the demonstrated irrelevant actions, we suggest that copying irrelevant actions may be influenced by social and causal cognition, resulting in an effective strategy which may facilitate acquisition of cultural norms when used discerningly.

Introduction

Children are prolific social learners and the extent of their faithful imitation of a model's behaviour is matched by no other species including other great apes (Dean, Kendal, Schapiro, Thierry, & Laland, 2012; Tennie, Greve, Gretcher, & Call, 2010; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). A wealth of previous research demonstrates that providing children with social information about a novel artefact can lead to the canalisation of behaviour, whereby children faithfully reproduce an observed behaviour without attempting possible alternatives (Flynn & Whiten, 2008a; Hopper, Flynn, Wood, & Whiten, 2010; Horner, Whiten, Flynn, & de Waal, 2006), sometimes leading to the copying of clearly causally irrelevant actions (Horner & Whiten, 2005; Wood, Kendal, & Flynn, 2012). Children's copying of irrelevant actions appears in different cultures (e.g. Kalahari Bushmen, Nielsen & Tomaselli, 2010 and western society, Horner & Whiten, 2005), increases with age (McGuigan, Whiten, Flynn, & Horner, 2007; Nielsen, 2006) into adulthood (Flynn & Smith, 2012; McGuigan, Makinson, & Whiten, 2011), and persists despite many forms of intervention (Lyons, Young, & Keil, 2007; Lyons, Damrosch, Lin, Macris, & Keil, 2011).

As children often receive social information regarding artefacts about which they have some degree of prior knowledge, the overarching aim of the current study was to understand how children's imitation of socially demonstrated solutions and causally irrelevant actions are influenced by experiencing multiple solutions to a problem.

When new social information contrasts with prior information children may draw upon 'social learning strategies', heuristics guiding their use of social information (Laland, 2004). Boyd and Richerson (1985) suggest that learning one solution can inhibit further exploration of a problem, with such conservatism common in non-human animals. Chimpanzees that discover one solution for food retrieval are unlikely to try a

more efficient solution and when one solution is precluded, those expert in the blocked solution do not adopt an alternative solution (Hrubesch, Preuschoft, & van Schaik, 2009). Similarly, Hopper, Schapiro, Lambeth and Brosnan (2011) found conservatism to initial social information even when an alternative behaviour, which was similar in difficulty, produced a higher value reward. Conservatism to personally acquired information continues in the face of equally beneficial alternate social information in a number of species (starlings, Templeton & Giraldeau, 1996; guppies, Kendal, Coolen, & Laland, 2004; sticklebacks, van Bergen, Coolen, & Laland, 2004; see Kendal, Coolen, van Bergen, & Laland, 2005 for a review). This reluctance to weight social information over personally acquired information can be overcome with sufficiently persuasive social information (nutmeg manikins, Rieucau & Giraldeau, 2009), costs to using personal information (fish, Kendal et al., 2004; orangutans, Lehner, Burkart, & van Schaik, 2011), or when individuals are allowed continued attempts to retrieve a reward (capuchin monkeys, Dindo, Thierry, de Waal, & Whiten, 2010).

We address children's use of these strategies by investigating children's behaviour after prior task experience and subsequent demonstrations of alternate task solutions which included causally irrelevant actions. Specifically, relating to differing solutions of an artificial-fruit task, we investigate: (1) how children weigh an initial socially demonstrated task solution with a subsequent socially demonstrated task solution, (2) whether personally acquired information affects children's copying of subsequent socially demonstrated solutions, (3) solution choice over time and (4) the influence of prior experience on the often prevalent reproduction of irrelevant actions.

Demonstrations of Alternative Solutions

Our first research question investigated how children weigh an initial socially demonstrated task solution with a subsequent socially demonstrated task solution. Traditionally, social learning studies have presented social information in the form of one or multiple demonstrations of the same solution, resulting in children faithfully copying the demonstrated solution in subsequent trials (Flynn & Whiten, 2008a, 2008b; Hopper et al., 2010; Horner et al., 2006). For example, Flynn and Whiten (2008a) found that only one child out of 80 attempted a solution that was different to the one witnessed. Similarly, in infancy use of a familiar tool is inflexible relative to a novel tool (Barrett, Davis, & Needham, 2007). Further, in studies of normativity children protest when an individual subsequently performs a behaviour that the child associates with a different, previously socially learnt behaviour (Rakoczy, Warneken, & Tomasello, 2008), suggesting that once a model demonstrates a solution children are quick to establish how something ‘ought’ to be done and do not accept the more recently demonstrated behaviour.

In contrast, Siegler and Opfer (2003) found that when working through mathematical problems children possess multiple numerical representations, such that a single child could utilise different methods to obtain the correct answer to similar problems. They suggested that children are motivated to acquire multiple strategies to solve a problem and that when similar problems are presented close in time children may use different solution strategies in their repertoire. In the current study, where some children were provided with social demonstrations of alternative solutions, we predicted that children would imitate the model’s first demonstration. We made no clear predictions about what children would do upon witnessing a second, alternative

solution. Such an investigation, however, is important as it reflects real-life learning and reveals the relative prevalence of solution canalisation and multiple strategy acquisition.

Personally Acquired Information

The relation between children's acquisition of knowledge through their own experience (personal learning) and through their interactions with others (social learning) has been of interest since the beginning of the empirical study of developmental psychology (e.g. Piaget, reviewed by DeVries (1997)). Adults can demonstrate an inherent resistance to changing their opinion (Ehlich & Levin, 2005) and although the number of, consensus among, and performance of demonstrators can result in adults disregarding their personal choice, participant confidence, success rate and non-public answers increase the probability of maintaining one's own choice (Asch, 1951, 1956; Morgan, Rendell, Ehn, Hoppitt, & Laland, 2012). Children with divergent personal information, regarding solutions to a reward extraction task, tend to converge upon a single solution in a social setting (Flynn & Whiten, 2010) suggesting children have some degree of social conventionality. If, however, social information is inaccurate (Clément, Koenig, & Harris, 2004), if the model is demonstrating an inefficient (Pinkham & Jaswal, 2011) or non-affordant method (DiYanni & Kelemen, 2008), or if the model has an 'unreliable' reputation (Ma & Ganea, 2010), children are more likely to rely upon their personally acquired information. Equally, when children are presented with a difficult experience of retrieving a reward, they copy an alternative technique (Williamson, Meltzoff, & Markman, 2008; Williamson & Meltzoff, 2011). Likewise, when a child's personally-acquired easy solution to a task becomes ineffective s/he defers to a model's task actions (Williamson et al., 2008). In the current study the difficulty or effectiveness of the solution was not manipulated. Therefore, the

current study makes a significant contribution to previous research by addressing children's relative weighting of prior, personally-acquired information against subsequent socially-acquired information when both provide solutions of comparable efficiency and validity. Due to the novelty of our research question we made no specific predictions regarding children's solution choice.

Solution Choice over Time

Traditionally, observational learning studies provide children with a single phase consisting of a demonstration of either a single (Lyons et al., 2007) or two or three (Flynn & Whiten, 2008b; Wood et al., 2012) demonstrations of the same solution, followed by a response phase. In the current study there were two phases of demonstrations (differing varieties) and responses consisting of two to seven trials. This allowed investigation of whether the number of solutions children experience and the source (personal/social) of those solutions affected their behaviour as their task experience increased. Whilst previous studies show canalisation to a demonstrated solution (as outlined above), there are rare instances of innovation and behavioural spread of such innovations (Whiten & Flynn, 2010) suggesting that as a child's experience with a task grows and as other solutions are witnessed s/he may be motivated to explore alternative solutions.

Irrelevant Action Imitation

There are conflicting theories as to why children imitate irrelevant actions. Lyons et al. (2011) suggest that when naïve children receive social information their causal beliefs become distorted by the demonstration of irrelevant actions to the extent that they believe that such actions are causally necessary. Alternatively, children may

not encode these actions as functionally necessary to acquiring the reward. Instead, they are unsure of the purpose of the actions and copy them as a default strategy which is refined later (Whiten, Horner, & Marshall-Pescini, 2005), or they interpret the model's actions as meaningful (Nielsen & Tomaselli, 2010), or normative (Kenward, Karlsson, & Persson, 2011; Kenward, 2012). Conversely, children may copy irrelevant actions to serve a social function of sharing an experience with a model (Užgiris, 1981) whereby children's social goals, identification with the model and with the social group in general, influences the copying of irrelevant actions (Over & Carpenter, 2012).

The current study aimed to discern between these explanations by asking a number of critical questions. First, does the social demonstration of two alternative methods lead to the extraction of only the critical sequences of actions required to reach a desired goal (Buchsbaum, Gopnik, Griffiths, & Shafto, 2011; Byrne, 1999)? Second, would children incorporate irrelevant actions presented in a demonstration that used the same solution as the children had themselves previously discovered? With both these questions, if the children omit the irrelevant actions it would suggest that the imitation of irrelevant actions may be due to adapted casual reasoning or, more simply, employ a strategy of 'copy now, refine later' (Whiten et al., 2005). Alternatively, if children copy these irrelevant actions faithfully it would suggest a more normative or social explanation. Third, does personally acquired experience decrease the copying of irrelevant actions of a previously unseen solution? Williamson et al. (2008) and Williamson and Meltzoff (2011) found that children with personally acquired success do not adopt an alternative technique involving the use of an opaque, causally irrelevant action. By presenting both an alternative solution and irrelevant actions within that solution we investigated whether children would be faithful to their previous solution, or whether they would adopt the new solution, either only including the relevant

actions, or in its entirety. If children imitate the alternative strategy but do not imitate the irrelevant actions it would suggest that there is an absence of social or normative motivation towards copying the puppet's irrelevant actions. Instead, their omission would suggest that children's personally acquired information gives them a casual understanding of the task (Lyons et al., 2011), or already refines their understanding of the task (Whiten et al., 2005) suggesting a more causal explanation for irrelevant action reproduction.

Summary

This study investigated how 5-year-old children behave after experiencing multiple solutions to a problem. Children of this age were chosen to allow for a comparison with related empirical work investigating imitation of tool use (e.g. Buchsbaum et al., 2011; McGuigan et al., 2010; Nielsen & Tomaselli, 2010; Wood et al., 2012). Our study adopted a two-action artificial fruit paradigm (Dawson & Foss, 1965; Whiten, Custance, Gomez, Teixidor, & Bard, 1996), the Sweep-Drawer Box (SDB, see Figure 1), a puzzle-box that contained a reward held in place by a series of defences. Critically, there were two separate solutions to the SDB, a drawer and a sweep mechanism that could be used to release the reward. Using a task with two possible solutions allowed a number of distinctions to be identified: (a) the propensity to discover each of these solutions during personal exploration, (b) the level of replication of a demonstrated solution compared to the level of production of an alternative solution, and (c) fidelity or exploration of solution use once an alternative solution was demonstrated. Irrelevant actions were incorporated into the demonstrations allowing investigation of whether personally acquired information, or multiple solution demonstrations, would reduce the copying of irrelevant actions. We made no specific

predictions regarding a child's solution choice or irrelevant action reproduction

following receipt of additional social information but such an investigation allowed us to examine such real-life contexts in a controlled manner.

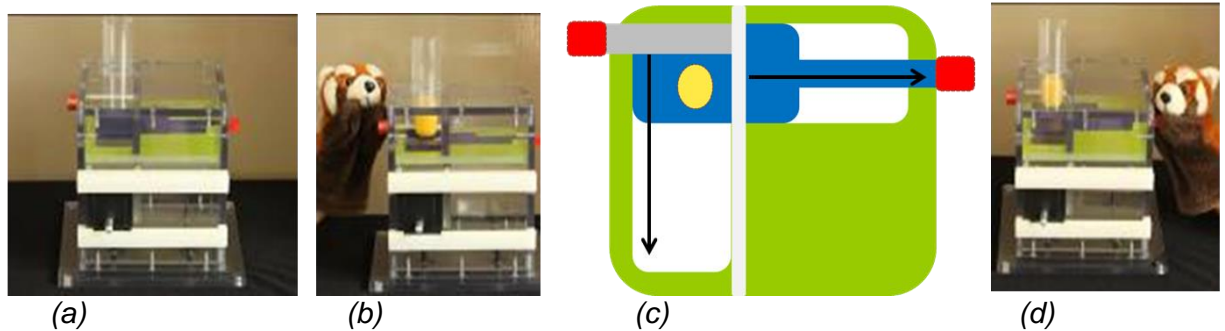


Figure 1. The Sweep-Drawer Box (panel a). Puppet using the sweep (panel b). Top view of SDB showing movement of sweep and drawer (panel c). Puppet using the drawer (panel d).

Method

Design

The experiment had two phases both consisting of task information and task interaction. Phase 1 manipulated the source of the child's original task information such that children either had personal or social experience. Phase 2 manipulated the subsequent task information such that successful children either had agreeing or opposing solutions or no further information and unsuccessful children either had their first demonstration or no further information. This design facilitated the investigation of children's behaviour after experiencing multiple solutions to a problem through the following assessments: (1) children's behaviour following alternative (Phase 1 and Phase 2) socially-demonstrated task solutions; (2) children's solution choice following personally acquired information (Phase 1) and subsequent social information (Phase 2);

(3) tracking solution choice over time (in multiple Phase 2 response trials); and (4) investigating the often prevalent reproduction of irrelevant actions following both phases.

Participants

One hundred and seventy children were recruited from eleven primary schools in County Durham, UK. Three participants were excluded from the study due to experimenter error leaving 167 (79 males, $M = 65.7$ months, $SD = 3.52$ months). There were no significant differences in sex [$\chi^2(7, N = 167) = 3.22, p = .86$] or age ($F_{7, 159} = 0.76, p = .62$) distribution across the eight conditions.

Apparatus

A two-action task, the ‘Sweep-Drawer Box’ (SDB, see Figure 1), was used. The SDB is a transparent box with an opening at the top where a capsule containing a reward (a sticker) can be inserted. After insertion the capsule falls onto an opaque platform where one of two spatially separated and functionally unique mechanisms can be manipulated in order to push the capsule to a lower level. These two manipulandi are, (1) a silver sweeper with a red handle (see Figure 1b) that when pushed moves the capsule to a hole through which the capsule falls to the lower level, and (2) a blue drawer with a red handle (see Figure 1d) that can be pulled outwards producing a gap through which the capsule falls to the lower level. Once in the lower level the capsule rests behind a black opaque door which can be opened to obtain the sticker. The capsule containing the sticker was inserted into the SDB by the experimenter with her left hand and on her right hand was a puppet, ‘Pip’. A puppet was used to avoid a model-based bias of copying the irrelevant actions of an adult model (see Wood et al., 2012). Whilst

there is a potential issue with the experimenter also being the controller of the puppet we found that children were markedly different in their reactions to Pip than they had been to the same experimenter in previous studies (Wood et al., 2012), instead their behaviour was similar to studies where a second experimenter had operated puppets (e.g. Rakoczy, Warneken, & Tomasello, 2009; Kenward, 2012). For example, participants exclaimed (when Pip performed irrelevant actions), ‘Silly Pip, why is Pip doing silly things?’ and (when demonstrating the alternate method), ‘Pip, you are cheating’. Although anecdotal, this suggests that the experimenter operating the puppet did not influence children’s copying any more than another adult operating the puppet.

Procedure

Children were tested individually at a table in a quiet area in their school. First the experimenter introduced the child to the puppet ‘Pip’ and completed a few easy tasks, such as finding stickers, to relax the child and introduce the concept of turn-taking with the puppet. The child was then asked to sit in front of the SDB and the experimenter said, “Today I have brought in this toy. I would like you and Pip to take turns to see if you can get the sticker out. Take a really good look at it. Can you see it Pip? (Pip nods). Can you see it (child’s name)?” The experiment then consisted of two phases which involved information acquisition and the child’s subsequent task interaction. Which condition a participant was placed into was determined by systematic allocation in Phase 1 (every third child was given social information, and the other two-thirds were given no initial social information), their subsequent behaviour in Phase 1 and systematic allocation in Phase 2 (with distribution partly predetermined to ensure correct participant numbers per condition). Due to high levels of personal success at

solving the task there were fewer children in no-information (Phase 1) conditions than personal (Phase 1) conditions. This design resulted in eight conditions (see Table 1).

In Phase 1 children were given either no information and were told, “You play with it first,” and progressed straight to the task interaction part of Phase 1, or were told, “It’s Pip’s turn first” and given a demonstration prior to interacting with the task themselves; the children watched as the experimenter put the capsule in the SDB and then used her other hand, with the puppet on, to extract the reward twice, both times using the same solution (see Figure 1). The puppet’s sequence of actions was as follows: the capsule was moved from the opaque level to the lower level using either the sweep or drawer solution. Immediately after the capsule fell a further five *irrelevant* actions were performed with whichever manipulandi was being used, either the drawer or sweeper, so that it was moved a further five times (forwards and backwards for the sweeper and in and out for the drawer). Then the door was opened and the capsule obtained.

After extraction, a sticker was put on Pip’s pile and the experimenter said, “That’s a sticker for Pip.” Demonstration of the two solutions (sweep or drawer) was counterbalanced across all conditions. Children then had two response trials, T1 and T2, and could interact with the task to successfully extract the reward using either the sweep or drawer solution (‘success’) or fail to extract the reward (‘fail’) after three minutes. Three minutes allowed sufficient time for success with the SDB but did not make unsuccessful participants uncomfortable. If required, the child was given prompts such as, “You can play with it as much as you like. You won’t break it.” They were never explicitly told to touch any part of the SDB. If successful in T1 a sticker was added to a child’s pile and the child was allowed a second trial (T2). The children’s behaviour partly determined which Phase 2 information they received.

In Phase 2 all children were told, “Now it’s Pip’s turn” and watched as the puppet did one of four things: (a) *No information* (conditions 3, 6 and 7a), in which the puppet looked at the SDB for 20 s but made no contact with it. Halfway through Pip was encouraged by the experimenter, “You can do whatever you like Pip, you won’t break it” and after 20 s the experimenter said, “I don’t think Pip wants a turn. It’s your turn now,” (b) *Agreeing* demonstration (conditions 2 and 5), in which the puppet extracted the reward twice, both times using the same solution as the child had used in Phase 1, (c) *Alternate* demonstration (conditions 1 and 4), in which the puppet extracted the reward twice, both times using the solution that the child had *not* previously used in Phase 1, and (d) *First demonstration* (condition 7b), 21 children who received no information and were unsuccessful in Phase 1, watched the puppet extract the reward twice using the same solution, with solution choice counterbalanced.

At the beginning of the task interaction trials in Phase 2 all children were told, “It’s your turn again. See if you can get the sticker out.” The child was allowed to interact with the SDB until s/he retrieved the reward successfully or three minutes had elapsed. If children were successful a sticker was added to their pile and they were told, “It’s your turn again,” until they had finished the maximum number of trials. The first 82 children tested were given two trials (T3, T4); at this point it became apparent that solution alternation was occurring and so the remaining 85 children were given five response trials (T3, T4, T5, T6, & T7) to investigate this further. At the end of testing all children were told they had done very well and were rewarded with stickers irrespective of their level of success.

Table 1: Overview of the six initial-success and two initial-failure conditions

| | Initial-success groups | | | | | | Initial-fail groups | |
|--|------------------------------------|-----------------------------------|------------------------|----------------------------------|---------------------------------|----------------------|---------------------|----------------------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7a | 7b |
| | Personal-then- social-alternate | Personal-then- social-agreeing | Personal-then- none | Social-then- social-alternate | Social-then- social-agreeing | Social-then- none | No information | None-then- social |
| Phase 1 | | | | | | | | |
| Information | No information | No information | No information | Demonstration | Demonstration | Demonstration | No information | No information |
| Response Trials | Success | Success | Success | Success | Success | Success | Failure | Failure |
| Phase 2 | | | | | | | | |
| Information | Alternate | Agreeing | No information | Alternate | Agreeing | No information | No information | Demonstration |
| Response Trials | T3 to T7 | T3 to T7 | T3 to T7 | T3 to T7 | T3 to T7 | T3 to T7 | T3 to T7 | T3 to T7 |
| Sample size (males) | 32 (17) | 21 (10) | 21 (11) | 21 (10) | 21 (11) | 21 (10) | 9 (3) | 21 (7) |
| Age months <i>M</i> (<i>SD</i>) | 66 (4) | 66 (3) | 66 (3) | 66 (4) | 66 (3) | 65 (4) | 64 (3) | 65 (4) |

Note. In Phase 1 children were given either (a) no information, “You play with it first” or social information (B) “It’s Pip’s turn first” and given a demonstration. Children then had two response trials, T1 and T2, and could interact with the task to successfully extract the reward (‘success’) or fail to extract the reward (‘failure’). In Phase 2 all children watched either (a) no information, (b) an agreeing demonstration, (c) an alternate demonstration or (d) a first demonstration (for those who had failed). Children then had two or five response trials.

Coding and Inter-rater Reliability

Each participant's performance was scored on three separate variables for each response trial, (a) success (sticker capsule removal), (b) solution used and (c) number of irrelevant actions copied (out of five). The experimenter, LW, coded 100% of the sample from video tape. An independent observer coded 26% of the sample. All Cronbach's Alpha scores were 0.90 or above, showing an excellent level of inter-rater reliability. All tests are two-tailed unless otherwise stated.

Results and Discussion

Following a brief description of behaviour of children who were initially unsuccessful, the results and discussion are presented in four sections: (1) the effect of demonstrations of alternative solutions upon children's subsequent solution choice, (2) the effect of personally acquired experience upon the imitation of subsequent socially demonstrated alternatives, (3) solution choice over time and (4) irrelevant action imitation.

Of the 104 children who witnessed no demonstration, 30 children (29%) were unsuccessful. In Phase 2, these children were given either no further information (condition 7a, $n = 9$) or a demonstration (condition 7b, $n = 21$). In the no further information condition, two of the nine children went onto successfully retrieve the reward. In the none-then-social condition, 20 of the 21 children successfully retrieved the reward after the demonstration, with all copying the solution witnessed, a statistically significant level of fidelity ($p < .001$, Binomial test). Fourteen of these 20 children copied an irrelevant action in T3, their first response trial in Phase 2. As the remaining two-thirds of children were able to retrieve the reward without social information, the SDB was challenging but within the capacity of most children.

Demonstrations of Alternative Solutions

The first research question focused on children's behaviour following demonstrations of alternative methods. In Phase 1 sixty-three children received a social demonstration and all were successful in Phase 1 response trials. Children who witnessed a demonstration were significantly more successful at T1 than children who had not witnessed a demonstration ($p < .001$, one-tailed Fishers Exact Test, FET). Sixty-two children (98%) used the same solution as they had witnessed in both T1 and T2 responses. In Phase 2, twenty-one children were allocated to the social-then-social-alternate condition. These children were more likely to use the demonstrated alternative ($N = 16$, 76% did so) than the originally demonstrated method ($p < .05$, Binomial test) in their first Phase 2 response (T3). This tendency to switch solutions was a result of the alternate social demonstration as children in the social-then-social-alternate condition were significantly more likely to use an alternative method in T3 than those in the social-then-none ($N = 21$, $p < .001$, FET) and the social-then-social-agreeing ($N = 21$, $p < .001$, FET) conditions, of which only 4 and 1 children respectively discovered a previously unused alternative.

Witnessing a demonstration led to a significant increase in success, relative to those who received no demonstration, with children imitating the specific solution used by the model. This supports the widely held view that children are prolific social learners who faithfully imitate (Whiten et al., 2009). The children receiving social information in Phase 1 were canalised to the socially demonstrated method in their Phase 1 response trials. However, when children with initial social information were shown an alternative solution of reward retrieval in Phase 2, the majority of them performed the newly demonstrated solution in their first subsequent Phase 2 trial which

stands in contrast to chimpanzees who fail to adopt subsequent social information (Hopper et al., 2011).

Personally Acquired Information

The second research question investigated whether the source of the prior information affected the copying of subsequent, socially demonstrated solutions. In Phase 1 seventy-four (71%) children who witnessed no demonstration were successful at retrieving the reward in both Phase 1 response trials. Forty-three used the drawer and 31 the sweep solution, indicating no natural bias in solution choice ($p = .201$, Binomial test). Sixty-three of these children (85%) used the same solution on both trials; however, eleven children switched solution between T1 and T2. Therefore, children with personal information were significantly more likely to find more than one solution in Phase 1 than children with social information ($N = 167$, $p < .01$, FET). These eleven children either had no further demonstration (personal-then-none) or a demonstration of one method (included in personal-then-social-agreeing). In Phase 2 thirty-two children were allocated to the personal-then-social-alternate condition. These children were more likely to use the demonstrated alternative solution ($N = 24$, 75% did so) than their personally discovered solution in their first task Phase 2 response (T3, $p < .001$, Binomial test). Multiple comparisons indicated that this tendency to switch solutions was a result of the social information demonstrated as children in the personal-then-social-alternate condition were significantly more likely to use an alternative method in T3 than those in the personal-then-none ($N = 15$, $p < .01$, FET) and personal-then-social-agreeing ($N = 16$, $p < .01$, FET) conditions, with 2 and 1 children respectively discovering a previously unused alternative.

Children with personally acquired information were more likely than children with prior social information to discover multiple solutions in Phase 1. Allowing children to interact with artefacts before social demonstrations may encourage exploratory behaviour. Children with personally acquired information have been shown to disregard subsequent social information if it is inaccurate (Clément et al., 2004), unreliable (Ma & Ganea, 2010) or unsuccessful (Williamson et al., 2008). In the current study the difficulty or effectiveness of the initial solution acquired was not manipulated, yet children in the personal-then-social-alternate condition were still motivated to copy the alternative solution, predominantly attempting the alternative demonstrated solution in their first subsequent interaction with the task. This use of social information, when personally acquired information is sufficient and not costly, contrasts with studies of our closest living relatives, chimpanzees (Hrubesch et al., 2009), and many other non-human species (Kendal et al., 2005). The demonstration appeared to be the key element in driving exploration as the vast majority of children with successful personally acquired information who received no further information, or social information that agreed with their personal information, did not discover the alternative solution. It could be argued that children who receive demonstrations of a solution in agreement with their prior solution may view the puppet as imitating the child. However, we deem this an unlikely explanation as children may be unaware that any alternatives exist and the puppet also includes irrelevant actions so does not faithfully imitate the child.

Table 2: Number (and %) of children who alternated their solutions in Phase 2 (excluding children who discovered two methods in Phase 1).

| Condition | Completed T3 & T4 (N = 125) | Phase 2: T3 and T4 | | | | Phase 2: T5-T7 | |
|--------------------------------|-----------------------------------|-------------------------------------|-----|--------------------------|-----|--------------------------------------|---------------------------------|
| | | Used a new solution in T3- T4 | | Two solutions T3 & T4 | | Completed T5, T6 & T7 (N = 76) | Used a new solution in T5-T7 |
| Personal-then-social-alternate | 32 | 27 | 84% | 19 | 60% | 15 | 1 |
| Personal-then-social-agreeing | 15 | 1 | 7% | 1 | 7% | 13 | 0 |
| Personal-then-none | 16 | 2 | 14% | 1 | 6% | 15 | 3 |
| Social-then-social-alternate | 21 | 18 | 86% | 8 | 38% | 7 | 0 |
| Social-then-social-agreeing | 21 | 1 | 5% | 0 | 0% | 15 | 0 |
| Social-then-none | 20 | 3 | 15% | 0 | 0% | 11 | 0 |

Solution Choice over Time

Our third question addressed whether children would be motivated to incorporate multiple methods into their repertoire. All 137 children in the six initial-success conditions were given at least two trials (T3 and T4) in Phase 2 and 76 of these children were given the opportunity to perform a further three trials (see Table 2). Multiple comparisons (Bonferroni corrected; $p = .017$) were made based on whether initial information had been personal or social. There was no difference between children in the social-then-social-alternate and the personal-then-social-alternate conditions in relation to which solution (original or newly demonstrated) was used at T3 ($N = 53$, $p = 1.0$, FET) or T4 ($p = .16$, FET) or whether they used the same solution for both T3 and T4 or two different solutions over these trials ($p = .17$, FET). Similarly, children with no information in Phase 2 (personal-then-none and social-then-none) did not differ from each other in their likelihood of using one or two methods in Phase 2 whether those children who discovered two methods in Phase 1 were included ($p = .05$, FET) or excluded ($p = .43$, FET). Children with agreeing information in Phase 2 (personal-then-social-agree and social-then-social-agree) did not differ from each other in their likelihood of using one or two methods in Phase 2 whether those children who discovered two methods in Phase 1 were included ($p = .23$, FET) or excluded ($p = .43$, FET).

Comparisons were also made based on whether children had received alternate, agreeing, or no information in Phase 2, regardless of the source of their initial information. Children who received an alternate demonstration in Phase 2 ($N = 53$) used the recently demonstrated solution, significantly more than chance at T3 (75%, $p < .001$, FET), but by T4, only 23 (43%) used the recently demonstrated solution which did not differ from chance ($p = .41$, FET). Twenty-seven of these 53 children used two

solutions in Phase 2 (T3 and T4 only) which was significantly different from the one child (out of 37) who did so from social-agreeing conditions (excluding those who discovered two methods in Phase 1; $p < .001$, FET) and the one child (out of 35) who did so from conditions receiving no information in Phase 2 (excluding those who discovered two methods in Phase 1; $p < .001$, FET). This difference between groups remained when analysing the 69 (excluding 9 that discovered two solutions in Phase 1) children that received five trials in Phase 2 [$\chi^2(2, N = 69) = 18.02, p < .001$].

In Phase 1, children with personal information were more likely than children receiving social information to discover multiple methods. However, by Phase 2 there was no difference in whether one or two methods were employed when comparing across matched conditions. For example, the majority of children who witnessed a social demonstration of an alternate solution regardless of Phase 1 information source alternated between the two solutions in Phase 2. This was markedly different to children who received no further information or social-agreeing information who predominantly used their original solution. It seems that personally acquired information encourages initial exploration and when children witness alternative strategies they are motivated to incorporate these solutions into their repertoire. The children did not appear to interpret the new solution as a ‘correction’, but rather a possible alternative. As in Siegler and Opfer (2003), children adopted multiple strategies to solve a single problem. It is important to note the exceptions in all of these conditions: ten children from conditions where no alternate social information was received found an alternative solution in Phase 2. Thus, whilst the initial response trials of those with prior social information mirrored the canalisation shown in studies providing children with one or two attempts at a task (Flynn & Whiten, 2008b; Horner et al., 2006), the current results indicate that continued interaction encourages exploration (Whiten & Flynn, 2010).

Irrelevant Actions

To begin this section the baseline production of the irrelevant actions is established. In Phase 1, of the children who were successful through acquiring personal information ($N = 74$), 19 (26%) performed an irrelevant action. Apart from one child who performed three irrelevant actions in T1, all others performed just one irrelevant action ($Mdn = 0.0$, $IQR = 0.0$, 0.0), resulting in the sweep or drawer being placed back to its original position, revealing a possible propensity to ‘tidy up’. Of those children who witnessed a demonstration including irrelevant actions in Phase 1 ($N = 63$), 54 (86%) performed an irrelevant action. Thirty-three of these 54 children (61%) performed more than one irrelevant action ($Mdn = 1.5$, $IQR = 1.0$, 5.0). Thus, despite the inclusion of ‘tidying up’ as an irrelevant action, children who witnessed a demonstration containing irrelevant actions produced significantly more irrelevant actions than those who did not in both T1 ($\chi^2(1, N = 137) = 57.61, p < .001$) and T2 ($\chi^2(1, N = 137) = 49.73, p < .001$).

A critical question was whether prior task experience would reduce the copying of causally irrelevant actions in subsequent response trials. This was addressed in a number of ways looking at Phase 2 behaviour. First, would children with two alternate social demonstrations copy irrelevant actions when attempting the second solution or would viewing multiple methods enable them to extract only the critical causal sequence of actions? For children in the social-then-social-alternate condition there was no significant change in whether a child performed an irrelevant action between Phase 1 (T2) and Phase 2 (T3; Binomial, $N = 21, p = .25$) and in the number of irrelevant actions produced between T2 ($Mdn = 1.0$, $IQR = 0.5$, 4.5) and T3 ($Mdn = 1.0$, $IQR = 1.0$, 4.0 , Wilcoxon $Z = -0.91, p = .93$). There was also no significant difference in the number of

irrelevant actions produced in T3 between children in the social-then-social-alternate condition and children in the social-then-none ($Mdn = 1.0$, $IQR = 0.0, 5.0$, $U_{(41)} = 176.5$, $Z = -1.20$, $p = .23$) and the social-then-agreeing ($Mdn = 1.00$, $IQR = 0.0, 5.0$, $U_{(41)} = 216.5$, $Z = -0.11$, $p = .92$) conditions.

Second, what actions will children with personally acquired information perform following subsequent social information including irrelevant actions? In the personal-then-social-agreeing condition six children (29%), who had not performed an irrelevant action in Phase 1, performed an irrelevant action in T3 (following a demonstration of the *same* solution). In this condition, whilst the number of children performing an irrelevant action did not increase significantly (McNemar, $N = 21$, $p = .13$), the number of irrelevant actions produced did increase significantly from Phase 1 (T2: $Mdn = 0.0$, $IQR = 0.0, 0.0$) to Phase 2 (T3: $Mdn = 0.0$, $IQR = 0.0, 1.00$, Wilcoxon $Z = -2.11$, $p < .05$). Similarly, for the 32 children in the personal-then-social-alternate condition, the number of children performing an irrelevant action increased significantly from T2 ($N = 6$) to T3 ($N = 16$; Binomial, $N = 32$, $p < .01$) as did the number of irrelevant actions (T2; $Mdn = 0.0$, $IQR = 0.0, 0.0$, T3; $M = 0.5$, $IQR = 0.0, 1.0$, Wilcoxon $Z = -3.16$, $p < .01$). Of the 24 children in this condition that attempted the alternative solution in T3, 12 (50%) used an irrelevant action. These 12 children performed a median of 1 ($IQR = 1.0, 3.0$) irrelevant action, which was not significantly different from the 16 children in the social-then-social-alternate condition ($Med = 1.0$, $IQR = 1.0, 4.0$, Mann-Whitney $U_{(28)} = 86$, $Z = -0.53$, $p = .60$).

For all 137 children in the initial (Phase 1) success conditions there was no significant difference, in the number of irrelevant actions produced, between T3 and T4 (Wilcoxon $Z = -1.71$, $p = .09$), and so children's mean scores across T3 and T4 were investigated across conditions (see Figure 2). Considering the mean number of

irrelevant actions in T3 or T4, there was no main effect of Phase 2 information for those with personal information in Phase 1 (personal-then-social-alternate/-agreeing/-none; Kruskal Wallis $\chi^2(2, N = 74) = 3.7, p = .16$) or for those with social information in Phase 1 (social-then-social-alternate/-agreeing/-none, T3: $[\chi^2(2, N = 63) = 1.27, p = .53]$). Therefore, conditions were collapsed according to the source of the original information. Children with personally acquired information performed significantly fewer irrelevant actions ($Mdn = 0.0, IQR = 0.0, 1.0$) than children with prior social information ($Mdn = 1.0, IQR = 1.0, 3.0$, Mann-Whitney, $U_{(135)} = 1108.0, Z = -5.51, p < .001$) during Phase 2 (T3 and T4).

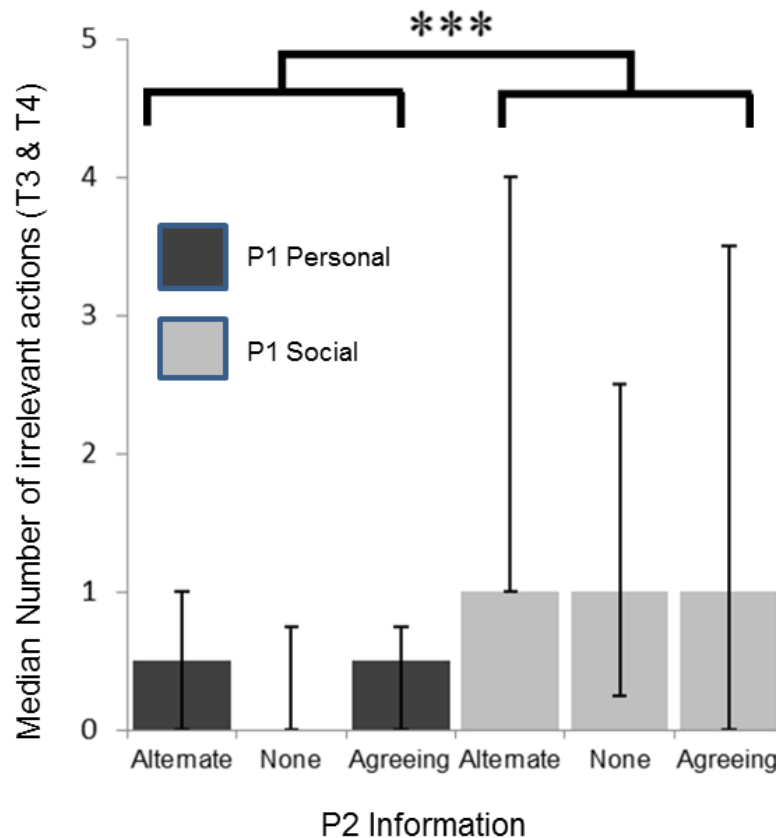


Figure 2: Median and interquartile range of mean number irrelevant actions (out of a possible five) in Phase 2 (Mean of T3 & T4) for the six initial-success conditions. P1 Personal; personal information in Phase 1, P1 Social; Social demonstration in Phase 1.

*** $p < 0.001$.

It appears that it is not prior experience itself which affects the copying of causally irrelevant actions but the type (personal or social) of prior experience. Those who had personal information in Phase 1 consistently performed fewer irrelevant actions than those who had social information in Phase 1. Children with prior social information continued to perform irrelevant actions regardless of the absence or presence of subsequent social information. Thus the copying of irrelevant actions was not affected by alternate demonstrations indicating that the children did not extract, from multiple alternatives, only the critical, causal sequence of actions to reach a desired goal (Byrne, 1999, Buchsbaum et al., 2011). We do not suggest that children are not capable of such efficiency but that in this context, involving different irrelevant actions pertaining to different solutions with the same artefact, the ability is constrained. Children with prior social information, who copy demonstrated actions and succeed, may be more likely to assume that copying of subsequent actions is a successful strategy in this context.

Successful prior-personal information appeared to give children both immunity and susceptibility to copying causally irrelevant actions. Of the children who produced no irrelevant actions at Phase 1, two-thirds (social agreeing) and half (social alternate) did not copy irrelevant actions following social demonstration. However, the remainder did and did so at a rate similar to children possessing prior-social information. The variance of behaviour of the children with prior-personal information suggests that irrelevant action reproduction may well be influenced by both the functional aspects of the task and social context. For example, possession of prior-personal, versus prior-social information may make children more sceptical about the function, whether social or causal, of observed causally irrelevant actions; possibly explaining why Williamson et al. (2008) and Williamson and Meltzoff (2011) found that children did not

incorporate subsequent (albeit opaque) irrelevant actions after a successful and easy experience with the task. However, for individuals in the prior-personal-social-alternate condition who did copy the demonstrated irrelevant actions, the unfamiliarity of the alternate solution may have resulted in children encoding the actions as causally relevant (Lyons et al., 2007) especially as more irrelevant actions were produced in this condition than where social information agreed with prior-personal information. As the task design ensured that these children already had a good understanding of the causal properties of the task we suggest, however, that children's copying of irrelevant actions in this context was more likely a result of motivation to adopt the model's seemingly purposeful (Nielsen & Tomaselli, 2010) or normative behaviour (Kenward et al., 2011; Kenward, 2012) or due to a motivation to share an experience with another (Užgiris, 1981). This highlights the persuasiveness of social information, even when emitted by a puppet and this persuasiveness may be adaptive if it enables acquisition of cultural norms.

General Discussion

The comprehensiveness of the current study enabled valuable insight into the role prior experience plays in children's social learning strategies pertaining to solution choice and imitation of irrelevant actions. Our results extend the field of social learning in a number of important ways. We found that children who are allowed to interact with a task before witnessing social demonstrations manipulate the task in more ways than those that witness an initial social demonstration. Further, after new solutions are discovered, whether through personal or social experience, children were motivated to incorporate these new solutions into their repertoire but they were not 'converted' to these alternatives, instead they switched between solutions. This multiple strategy use is

seen in other domains in children's learning, such as mathematics (Siegler & Opfer, 2003) and continues into adulthood (Dowker, Flood, Griffiths, Harriss, & Hook, 1996). Adopting further strategies when one already has a successful strategy may seem cognitively inefficient, but there are several reasons why it is beneficial. First, learning about a new strategy is useful in the event that an original strategy fails. Second, learning multiple strategies increases one's overall knowledge of the task and provides generalisable knowledge regarding the properties of each strategy and the affordances of different manipulandi. In a tool-abundant culture the latter is valuable knowledge. Third, a motivation to acquire additional knowledge enables modifications over time. This 'ratchet effect' has been speculated to be the bedrock of cumulative culture, a process thought to be unique to humans (Dean et al., 2012; Tennie, Call, & Tomasello, 2009).

The current study also makes a valuable contribution to our understanding of the phenomenon of copying causally irrelevant actions. Overall, children who hold personal information about a task are less likely than those receiving only social information to incorporate causally irrelevant actions after observing them displayed by others. Children with initial social information faithfully copy causally irrelevant actions even after continued personal task interaction and despite the fact that the actions occurred with a transparent box (revealing the irrelevance of the actions) and *after* the relevant action (the reward capsule had been successfully moved to the lower level barrier) as has been found previously (Simpson & Riggs, 2011). Successful prior-personal information appeared to give some children immunity from copying causally irrelevant actions whilst other children were still susceptible to copying these actions, illustrating that the copying of causally irrelevant actions is an intricate phenomenon and no one explanation may capture its complexities. Children's solution choice, their reasoning

about causality, their motivation to share an experience with a model and the pressure to conform to norms will all vary depending upon task difficulty (Williamson & Meltzoff, 2011), the number of models (Asch, 1951), the characteristics of the model(s) (Wood et al., 2012), the audience (Haun & Tomasello, 2011) and, as has been shown in the current study, the prior information a child has regarding a task. These variables can be addressed individually or in combination and will enable a better understanding of children's motivation to learn certain aspects of a task from others. Studies that establish the complexity of children's social learning will shed more light on how and why humans stand alone in the breadth, detail, and cumulative nature of their culturally-rich world.

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Chapter V

Familiar peers' past-proficiency and children's task solution choice

This chapter focusses on the interaction between a model-based bias of past-proficiency and multiple demonstrations and personal task interactions. This chapter is to be submitted to PLoS ONE with the same order of authorship (Lara A. Wood, Rachel L. Kendal and Emma G. Flynn).

Abstract

The current study investigated whether four- to six-year-olds' tool-use task solution choice was influenced by a child's prior experience with the task and/or the past-proficiency of familiar peer models. We completed behavioural assessments of interactions with novel tasks provided to freely interacting classes of children in four primary schools. Additionally, peer and teacher predictions of each child's proficiency with novel artefacts were obtained. Based on these assessments, two models from each of the four classes, matched on sex, age, dominance and popularity, were selected. One of the selected models for each class had a high past task proficiency while the other had a low past-proficiency. Video recordings of these trained models removing a reward, in one of three ways, from an artificial-fruit task using causally relevant and irrelevant actions, were shown to peers after the peer had either a successful, unsuccessful or no interaction with the task. Results indicated that children were motivated to incorporate multiple solutions into their repertoire, and that acquiring multiple methods might supersede a past-proficiency model-based transmission bias. However, when one model matched a child's solution and one model offered an alternative solution children were biased towards selecting the solution choice of the model with the highest past-proficiency.

Introduction

Children employ a number of transmission biases (Boyd & Richerson, 1985) or social learning strategies (Laland, 2004), influencing the circumstances under which children copy. Whilst naïve children with no prior experience of a novel artefact are prone to behavioural canalisation and copying of irrelevant actions (Horner & Whiten, 2005), children with prior experience show flexibility in their task solution choices, often experimenting and incorporating many solutions into their repertoire (Siegler & Opfer, 1996; Wood, Kendal, & Flynn, 2013), switching solutions when personally-acquired solutions are difficult or become redundant (Williamson, Meltzoff, & Markman, 2008; Williamson & Meltzoff, 2011), and omitting irrelevant actions (Wood et al., 2013).

Children also demonstrate model-based biases in their learning (Wood, Kendal, & Flynn, submitted) whereby traits copied by individuals are influenced by the characteristics of the model, such as their age or familiarity. Here, we implemented an experimental procedure designed to mirror a naturalistic context to address three aims: first, to better understand children's solution choices given their personal experience with a task; second, to investigate the degree to which they behaved according to a past-proficiency model-based bias; and third, to understand the relation between prior experience and a past-proficiency model-based bias. We expand on these aims in the following three sections.

Prior Experience and Solution Choice

When social learning studies have presented social information in the form of one or multiple demonstrations of the same solution, naïve children faithfully copy the demonstrated solution in subsequent trials (Flynn & Whiten, 2008a, 2008b; Hopper, Flynn, Wood, & Whiten, 2010; Horner, Whiten, Flynn, & de Waal, 2006). However, if

children have prior experience with a task which afforded them easy solutions, they are less likely to copy a subsequent, socially demonstrated, alternative technique with non-functional actions as compared to children with a difficult prior personal interaction (Williamson et al., 2008; Williamson & Meltzoff, 2011). Furthermore, children who interact with a task before witnessing social demonstrations are more likely to discover multiple solutions, and after new solutions are discovered or observed children are motivated to incorporate these new solutions into their repertoire (Wood et al., 2013). This multiple solution use is seen in other domains in children's learning, including mathematics (Siegler & Opfer, 1996) and continues into adulthood (Dowker, Flood, Griffiths, Harriss, & Hook, 1996).

Although acquiring new solutions when one has a successful solution may seem inefficient, learning new solutions is useful in the event that an original solution fails, and it increases one's overall knowledge of the task potentially providing generalisable knowledge regarding the properties of each solution. Developing skills which are immediately unnecessary but may assist in a changing environment are thought to underpin instances of contrafreeloading where children (Singh, & Query, 1960) and other animals (Jensen, 1963) work for 'earned' rewards even though identical 'free' awards are available (Inglis, Forkman & Lazarus, 1997). Moreover openness to adopting multiple solutions to a challenge may partially underpin cumulative culture which is widely held to be responsible for the success of humanity as a species (see Dean, Vale, Laland, Flynn, Kendal, submitted). We predicted that children who discover a solution through personal exploration and subsequently observe alternate solutions will try one of these alternate solutions on their first subsequent attempt and will ultimately incorporate all solutions into their repertoire. In accordance with Wood et al. (2013), we also predicted that children with successful prior personal experience

would copy significantly fewer irrelevant actions than children with unsuccessful or no prior experience.

Past-Proficiency Model-based Bias

When faced with divergent information from numerous individuals it is adaptive to have a strategy as to whose information one should copy. Children demonstrate such model-based biases in their learning (Wood et al., submitted). For example, children are more likely to imitate all actions demonstrated by an adult versus a child model when the model is demonstrating novel behaviour (McGuigan, Makinson, & Whiten, 2011; Seehagen & Herbert, 2011; Wood, Kendal, & Flynn, 2012; although the opposite pattern is observed when the actions are familiar, Zmyj, Daum, Prinz, Nielsen, & Aschersleben, 2011). Children also preferentially copy models who are most similar to them (e.g. same- over opposite-sex models; Frazier, Gelman, Kaciroti, Russell, & Lumeng, 2011; Shutts, Banaji, & Spelke, 2010), perhaps because they provide the most relevant information.

A model's success in a particular environment indicates an ability to thrive within that environment. As stated earlier, but for emphasis, Rendell et al (2011) describes model-based biases relating to success. This refers to instances in which learning may be biased towards copying (a) if the payoff is better, (b) in proportion to the payoff or (c) the most successful individual. However, it is unclear whether these instances are occurring in the present, i.e. as the model is demonstrating the information which may be transmitted, or in the past i.e. that the success was demonstrated in the past and that some form of 'success reputation' is biasing subsequent information transmission from model to observer. Furthermore, it is not clear whether success relates to domain specific model success relating to the specific information which is to

be transferred or whether it is domain general success i.e. that the model generally has more success in his/her environment which may also be related to dominance and prestige (Henrich & McElreath, 2003).

Therefore, we use the term past-proficiency to refer to a model's domain-specific ability shown in the past. As such it focusses on the potential for a model to have a reputation for being skilled within the domain in which the model is currently demonstrating. It is the influence of a model's past proficiency that the current study investigates. The current study used a series of novel artefacts, so proficiency referred to *successful interaction with novel artefacts*. Therefore, our models had either a high past-proficiency or a low past-proficiency pertaining to the degree of exploration or, where appropriate, successful extraction of stickers with a series of novel artefacts. Research has demonstrated that infants are able to discriminate between unfamiliar models who act successfully versus incompetently (Zmyj, Buttelmann, Carpenter, & Daum, 2010) and seven-year-olds preferentially copy children rated by an experimenter as being competent rather than less competent (Brody & Stoneman, 1985). Indeed, from infancy to six-years, children consistently copy reliable, over unreliable, models for labelling (Koenig, Clément, & Harris, 2004; Koenig & Harris, 2005b; Vázquez, Delisle, & Saylor, 2012) and artefact use (Birch, et al., 2008; Zmyj et al., 2010).

Laboratory experiments with unfamiliar models enable a controlled investigation of social learning. However, it is also beneficial to look at children's behaviour 'in the wild' (Flynn & Whiten, 2010). Here, studies implement a controlled design in a naturalistic setting, such as a classroom, thus, using familiar models. For example, open-diffusion studies, where a known model demonstrating a behaviour is introduced to a group of familiar novices, represents a realistic and ecologically-valid context in which to explore social learning and cultural transmission (Flynn & Whiten,

2012; Dean, Kendal, Schapiro, Thierry, & Laland, 2012). Using this methodology Flynn & Whiten (2012) showed that characteristics of known peers may bias social learning; children interacting with a task were watched more if they were older rather than younger, liked over not-liked or more dominant over less dominant. In the current study we selected two familiar peers to serve as models. These children were either high in past-proficiency (high past-proficiency model; High PPM) or low in past-proficiency (Low PPM) relating to interaction with novel artefacts. We predicted that naïve children (no prior experience) who observed differing solutions would preferentially copy the solution choice of the High PPM over the Low PPM.

Interaction between Prior Experience and Past-proficiency

Children's personal experience may also influence model-based biases. For example, children may exhibit a preference for the new modelled solution irrespective of model identity. Alternatively, if a model matches a child's solution this might influence the child to stick to his/her original method, as seen in Wood et al., (in press). Finally children's decision to try a new solution or remain with their own solution may be influenced by the past-proficiency of the model. By including conditions in which children were allowed to interact with the task before witnessing demonstrations, the current study investigated the interaction between prior experience and past-proficiency biases relating to solution choice. We made two predictions: first, children who discover a solution and witness two alternatives from the two models will be motivated to try all solutions but over time will preferentially copy the solution choice of the High PPM over that of the Low PPM. Second, children who discover a solution and subsequently observe a model matching their choice and one model offering a novel solution, will be

more likely to deviate from their original solution if the alternative is offered by the High PPM versus the Low PPM.

Summary

The current study had three aims: first, to better understand the children's solution choices given their personal experience with a task; second, to investigate a past-proficiency model-based bias; and, third, investigate the relation between prior experience and solution choice. The study required the selection of known models with differing levels of task past-proficiency. Children's proficiency was assessed with novel tasks similar to the test task. Task past-proficiency was established through peers observing each other interacting with these tasks and through peer (Flynn & Whiten 2012) and teacher (Pellegrini, et al. 2007) ratings of proficiency. To investigate whether proficiency ratings were confounded by dominance and popularity, children and teachers also rated peers/pupils on these traits. This model selection was rigorous (see Table 1) and so we present a concise Method and Results section for model selection here followed by the Method and Results section for the main experiment.

Model Selection: Method

Participants

One hundred and ten children (59 males), aged between 56 and 80 months ($M = 65.52$, $SD = 6.00$), were recruited from four primary school classes in County Durham, UK. The children had been in their classes for between eight and nine months. Five children were absent on the day of collecting peer ratings. Ten members of staff across the four classes assisted with the study. They were all female and worked full time with the respective classes either as the class teacher or as a teaching assistant, all are

henceforth described as teachers. The class sizes were as follows: class A = 23 (12 males), class B = 27 (14 males), class C = 28 (13 males), and class D = 32 (20 males). There were no significant differences in the number of boys or girls in each class (Binomial $p > .5$).

Apparatus



*Figure 1a. **Easy-Reward; Sticker Pipe.** 150cm long white Perspex pipe with a larger hole ($d = 10\text{cm}$) at one end and 12 smaller holes ($d = 3\text{cm}$) along the pipe. The pipe was filled with shredded paper, and approximately 100 stickers. The stickers could be removed from the holes. This task was designed to be easy with potentially all stickers being accessed in a 20min session.*



*Figure 1b. **Difficult-Reward; Sticker Disc.** 25cm x 25cm x 5cm (h x w x d) transparent Perspex box with six compartments containing shredded paper and around 100 stickers. Each compartment had a hole ($d = 3\text{cm}$) at the front. On the front of the box was a circular transparent Perspex disk ($d = 25\text{cm}$) with four holes ($d = 3\text{cm}$). This circular panel could rotate, allowing for the panel hole and the compartment hole to line up for potential access to the stickers. Two plastic tweezers were attached by a 30cm length of flexible wire and could be used to obtain the stickers. This task was designed to be challenging with potentially only a few stickers being accessed in a 20min session.*



*Figure 1c. **No-Reward; Balls of Fun.** 100cm long transparent Perspex pipe filled with twelve balls of differing colours, sizes and textures including three that could be used as whistles. The pipe had three long thin holes cut into it ($l = 10\text{cm}$, $w = 2\text{cm}$) so that children could touch the balls but the balls could not be removed from the pipe.*

Table 1 Overview of assessments

| Trait | Name | Source | Method of assessment |
|-------------|---------------------------|---|--|
| Proficiency | No-Reward | Novel tasks: interactions during 15- 20m of free play | Behavioural assessment of interaction including order (relative to the other children) of first proximity (within 1m and oriented towards the task), interaction (placing their hands on part of the task) and success (removing a sticker from the task in the reward tasks). |
| Proficiency | Easy-Reward | | |
| Proficiency | Hard-Reward | | |
| Proficiency | Proficiency | Peers: Asked to pick up to five classmates from photos | Asked, 'Which five children would be really good at getting the sticker out of this box?' |
| Popularity | Popularity | | Asked, 'If you could take five children to a party, who would you take?' |
| Dominance | Dominance | | Asked, 'Are there any children who like to tell other children what to do?' |
| Proficiency | Proficiency | Teachers: Asked to place photos of children into one of five groups (Likert scale) for each of the six adjectives | Inquisitive: Likely to explore this task |
| Proficiency | Proficiency | | Intelligent: Quick and accurate in judging and comprehending this task |
| Proficiency | Proficiency | | Inventive: Likely to engage in an inventive behaviour with this task |
| Popularity | Popularity | Aggressive Dominance | Friends with a significant number of others/a smaller number of more influential individuals |
| Dominance | Dominance | | |
| Dominance | Unaggressive Dominance | | |
| | | | Able to acquire and monopolise resources over other individuals |

Behavioural Proficiency: Assessment and Results

At the beginning of testing in each school the children were told that new toys would be available in ‘free-play’ and all children were allowed to interact with these as much as they liked but they could also choose a different activity if they wished. Each novel task was made available to the whole class during these free play 15-20min sessions. They were also told that cameras would be recording them, one video camera was placed 2m behind the task and another was placed 1m to the side of the task. The experimenter (LW) stood by the side camera and provided a discrete commentary identifying children and describing behaviours to aid subsequent coding.

For coding, children’s order (relative to the other children) of first proximity (within 1m and oriented towards the task), interaction (placing their hands on part of the task) and success (removing a sticker from the task in the reward tasks) were recorded. Additionally, the frequencies of proximity, interaction and success were recorded using one-zero sampling, whereby the occurrence or absence of each behaviour was noted within 30 second intervals. Scores are expressed as the proportion of the potential 40 thirty-second intervals that a child was in proximity to, interacting or succeeding with the task. Finally, children were scored for the number of different types of interactions with the task (e.g., for the No-Reward task a child could touch the task, insert finger into slit, move ball with finger, move whole tube, interact with the lid, and interact with the zip-ties attaching the task to a rack, and number of stickers obtained (reward tasks). A lower rank equated with more Task Success.

Pearson rank correlations for behaviour with each of the novel tasks demonstrated that each child’s behaviour was similar across the three tasks. Scores on the No-Reward task were positively correlated with scores on the Difficult-Reward task ($r_{99} = .42, p < .001$) and Easy-Reward task ($r_{101} = .26, p < .01$) which also positively

correlated with the Difficult-Reward task ($r_{103} = 0.60, p < .001$). On occasion children were absent during the presentation of one of the novel tasks so the scores for each task were kept separate. The dependent variables of performance with each of the three tasks was entered separately into a stepwise linear regression along with the child's sex (male = 0 or female = 1) and age (in months). Sex and age were not significant predictors of Task Success for the No-Reward task. However, for the Difficult-Reward task, age (but not sex) was a significant predictor ($\beta = -0.271, t_{101} = 3.79, p < .001$) of Task Success with older children receiving better (lower) ranks. For the Easy-Reward task both age ($\beta = -0.30, t_{103} = -2.71, p < .01$) and sex ($\beta = -6.66, t_{103} = -4.87, p < .001$) were significant predictors of Task Success with older children performing better (lower ranks) than younger children and females performing better than males. To summarise, children showed behavioural consistency across the three tasks and older children and girls tended to be more proficient than younger children and boys.

Peer Ratings: Assessment and Results

Individually, children were presented with an artificial fruit used in previous social learning research (the transparent version of the Glass Ceiling Box, (GCB) see Horner & Whiten, 2005). Children were given a single demonstration of how to retrieve a sticker (by lifting a door, inserting a Velcro topped stick and attaching it to a Velcro sticker) by the experimenter (LW); the demonstration did not include causally irrelevant actions which are typically presented with this task. Then children were told it would be their turn after they had answered some questions about their classmates. On a table in front of the participants lay photos of all their classmates, and children were asked three questions; first, one relating to peer proficiency, "Can you tell me which five children would be really good at getting the sticker out of this box?", second, one relating to peer

popularity, “If you could take five children to a party with you, who would you take?”, third, one relating to peer dominance, “Are there any children who like to tell other children what to do?” (For the last question children struggled to pick five, therefore the question was adapted so children could pick between zero and five peers). The children were then asked again, “Do you remember that I asked who would be really good at getting the sticker out? Can you pick those five children again?” This repetition was to ascertain whether responses were consistent over a short amount of time. For each question, the experimenter noted the identity of the five children and then shuffled the photos and randomly distributed them across the table before the next question was asked. At the end of the questioning children were invited to interact with the GCB and were then given a sticker. All children were successful and this interaction was not recorded but served as a means of rewarding children for their participation.

Of the 105 children who responded 42 (40%) failed to be consistent in their assessment of peer proficiency, that is, they did not choose at least three of the same five children at the beginning and at the end of the session when asked the same question. Despite a similar number of boys and girls, significantly more boys ($M = 5.98$, $SD = 2.80$) were selected as proficient than girls ($M = 4.06$, $SD = 2.81$; $t_{104} = 3.53$, $p < .01$). However, there was an interaction between sex of peer and sex of participant with boys choosing more boys ($M = 7.37$, $SD = 2.14$) than girls ($M = 4.33$, $SD = 2.61$; $t_{103} = 6.55$, $p < .001$) and girls choosing more girls ($M = 5.65$, $SD = 2.58$) than boys ($M = 2.72$, $SD = 2.27$; $t_{103} = -6.18$, $p < .001$). Children’s proficiency score (\sum peer selections) were entered into a stepwise linear regression in which sex (male = 0 or female = 1), age (in months), popularity (\sum peer selections) and dominance (\sum peer selections) were entered as predictors. Age was the only significant predictor of proficiency rating ($\beta = 1.11$, $t_{108} = 6.92$, $p < .001$) with older children receiving more

proficiency nominations than younger children. Sex ($\beta = -0.15$, $t_{108} = -1.85$, $p = .07$) and popularity ($\beta = 0.14$, $t(108) = 1.74$, $p = .08$) approached significance with males and more popular children being selected more often as proficient. Dominance was not a significant predictor ($\beta = 0.01$, $t_{108} = -0.14$, $p = .99$) of proficiency. To summarise, children were not consistent in their choices of proficiency of their peers and tended to rate older, more popular, children of the same sex as themselves as proficient.

Teacher Ratings: Assessment and Results

Teacher's ratings were used to assess the validity of measuring children's proficiency with the novel tasks. Teachers were shown the transparent GCB as an example of a novel task and asked to place photos of the children into one of five groups: 1 (not at all like this child), 2 (not like this child), 3 (neither like nor not like this child), 4 (like this child), and 5 (very like this child). The first statements related to proficiency and required teachers to rank children according to: inquisitive, defined as, *Likely to explore this task*; intelligent, *Quick and accurate in judging and comprehending this task*; and inventive, *Likely to engage in an inventive behaviour with this task*. Teachers were also asked to rank children on popularity (*Friends with a significant number of others/a smaller number of more influential individuals*), aggressive-dominance (*Often initiate conflicts with other children and dominates resources*) and unaggressive-dominance (*Able to acquire and monopolise resources over other individuals without using aggression*). These questions were based on constructs developed by Freeman et al. (submitted). The scores of same-class teachers were significantly positively correlated with each other for each trait (Table 2) with the exception of some of the ratings from teachers from Class A, possibly due to the smaller size ($N = 23$). As there was agreement amongst the teachers, children received a mean

score for each of the six traits. As the three proficiency adjectives were positively correlated (inquisitive with intelligent; $r_{110} = .44, p < .001$, and inventive; $r_{110} = .56, p < .001$, inventive with intelligent; $r_{110} = 0.71, p < .001$) they were combined into a single construct of proficiency.

Teachers' mean proficiency ratings were entered into a stepwise linear regression to assess the possible predictive power of a child's sex (male = 0 or female = 1), age (in months), popularity, aggressive and unaggressive dominance. Age ($\beta = 0.59, t_{107} = 0.89, p = .38$) and sex ($\beta = 0.11, t_{107} = 1.73, p = .09$) were not significant predictors of teacher ratings of proficiency although sex approached significance with girls receiving a higher rating score ($M = 9.96, SD = 3.13$) than boys ($M = 8.80, SD = 3.29$). Teacher ratings of popularity ($\beta = 1.22, t_{107} = 6.02, p < .001$), aggressive ($\beta = -0.91, t_{107} = 5.50, p < .01$) and unaggressive dominance ($\beta = 1.48, t_{107} = -3.55, p < .001$) were all significant predictors of proficiency, with increased affiliation and unaggressive dominance ability scores, and decreased aggressive dominance scores, predicting increased proficiency scores. To summarise, it appears that teachers' proficiency judgements were not influenced by children's age or sex, but corresponded positively with ratings of popularity and unaggressive dominance.

C: Teacher correlations*Table 2: Correlations for teachers' rating of children's traits in each of the four classes*

| | Inquisitive | | Intelligent | | Inventive | | Popularity | | Aggression | | Unaggressive Dominance | |
|-----------------------|-------------------|-----------|-------------|-----------|-----------|-----------|------------|-----------|------------|-----------|------------------------|-----------|
| | Teacher 2 | Teacher 3 | Teacher 2 | Teacher 3 | Teacher 2 | Teacher 3 | Teacher 2 | Teacher 3 | Teacher 2 | Teacher 3 | Teacher 2 | Teacher 3 |
| Class A: Teacher 1 | 0.46 ⁺ | 0.78* | 0.59* | 0.79* | 0.37 | 0.22 | 0.49 | 0.64** | 0.61* | 0.62 | 0.49+ | 0.84** |
| Class B: Teacher 1 | 0.50** | NA | 0.71*** | NA | 0.81*** | NA | 0.45* | NA | 0.66*** | NA | 0.60** | NA |
| Class C: Teacher 1 | 0.48** | NA | 0.74*** | NA | 0.31 | NA | 0.72*** | NA | 0.88*** | NA | 0.50** | NA |
| Class D: Teacher 1 | 0.70*** | 0.51** | 0.79*** | 0.39* | 0.83*** | 0.74*** | 0.56** | 0.53** | 0.63*** | 0.39* | 0.62*** | 0.58*** |

Note. * $p < .05$, ** $p < .01$, *** $p < .001$ ⁺ $p < .075$

Relation between Peer and Teacher Ratings and Behavioural Proficiency

Success scores with the three novel tasks were entered separately as dependent variables into a stepwise linear regression with teacher and peer ratings, sex and age, as predictor variables (Table 3). For the Easy-Reward task, the model accounting for the most variance (31.7%) of Task Success included teacher's proficiency ratings, sex and age; children with higher teacher's proficiency ratings, girls and older children had more Task Success than those with lower proficiency ratings, boys and younger children respectively. For the Difficult-Reward task, teacher's proficiency ratings was the only variable in the best model which accounted for 14.7% of the variance of Task Success; children with higher proficiency ratings from teachers had more Task Success than those with lower proficiency ratings. For the No-Reward task, no variables were significant predictors.

Table 3: Linear Regression (Stepwise) predicting Task Success on novel tasks

| Variables in Equation | Easy-Reward | | | | Hard-Reward | | | |
|-----------------------------|-------------|------|---------|----------|-------------|------|---------|----------|
| | B | SE | β | <i>t</i> | B | SE | β | <i>t</i> |
| Constant | 38.54*** | 9.98 | | 5.51 | 22.79*** | 2.19 | | 10.42 |
| Teacher proficiency ratings | -0.79*** | 0.01 | -0.33 | -3.86 | -0.95*** | 0.22 | -0.39 | -43.3 |
| Age (months) | -5.68*** | 1.31 | -0.36 | -4.34 | | | | |
| Sex (Male = 0, Female = 1) | -0.22* | 0.11 | -0.17 | -2.04 | | | | |

Selecting Models

Our original intention was to select models based on (1) behaviour with the novel tasks as children could witness the relative success of their peers, and (2) peer ratings of proficiency in order to reflect children's perception of each other. However, children were not consistent in their ratings of their peers over a short time period. Conversely, children's behaviour with the three novel tasks was consistent demonstrating that children's novel task proficiency was robust. Furthermore, teacher ratings of proficiency correlated with

performance on both reward tasks. We, therefore, modified the design such that behavioural performance, supported by teaching ratings, was prioritised over peer ratings for the choice of models. As age and sex had correlated with peer proficiency ratings and popularity and dominance had correlated with staff proficiency ratings, models were age, sex, popularity and dominance matched within each class.

The High PPM was chosen from children who reached the following criteria: ranked in the top five children for Task Success in at least two of the novel tasks and ranked in the top five children for teacher proficiency rankings. The Low PPM was chosen from children who reached the following criteria: matched the High PPM in sex and age (within 60 days), ranked in the bottom ten children for teacher proficiency ratings, did not come in the top ten children for Task Success with any novel task and came in the bottom five for at least one novel task. This was possible for three of the four classes, in the fourth class (Class B) no child reached these criteria so a child who was ranked in the top five children for proficiency by the teachers, and was ranked 6th and 12th in two novel tasks was selected as the High PPM model and a child who was ranked 12th from bottom (out of a possible 27) in teacher proficiency and who met the previously described novel task criteria, was selected. All analysis was run with data from this class included and excluded and the results remained the same. The models were also closely matched for popularity and dominance. For popularity, the range of all children's scores was between 0 and 15 peer-selections. For all classes there was no more than two peer-selections difference between models. For dominance, the range of all children's scores was between 0 and 7 peer-selections. For three classes there was no more than two peer-selections difference, in the final class there was a difference of three peer selections (see Table 4).

Table 4: Overview of the eight models, two selected from each class

| Class | Model | Sex | Age | Novel Task Ranks (Class Median) | | | Teacher Scores (Class Median) | | | | Peer Scores (Class Median) | | |
|-------|-------|-----|-----|---------------------------------|-------------|--------------------|-------------------------------|------------|------------|----------------|----------------------------|-------|-------|
| | | | | No | Difficult | Easy | Proficiency | Popularity | Aggressive | Non-aggressive | Peer | Peer | Peer |
| | | | | Reward | Reward | Reward | | | Dominance | Dominance | | | |
| A | High | M | 65 | 3 (12.5) | 3.5 (10.5) | 14 (12.5) | 14 (9.3) | 5 (3.5) | 3 (2.5) | 4 (3) | 11 (8) | 6 (5) | 2 (4) |
| | Low | M | 64 | 20 (12.5) | 12 (10.5) | 12.5 (12.5) | 9 (9.3) | 5 (3.5) | 2 (2.5) | 5 (3) | 10 (8) | 7 (5) | 1 (4) |
| B | High | F | 59 | 12 (14) | 6 (14) | 10 (14) | 15 (9) | 5 (3) | 5 (2.5) | 5 (3) | 7 (9) | 4 (3) | 3 (2) |
| | Low | F | 60 | 22 (14) | 23 (14) | 11 (14) | 10 (9) | 3 (3) | 4 (2.5) | 4 (3) | 5 (9) | 6 (3) | 2 (2) |
| C | High | M | 65 | 4 (12.5) | 2 (12.5) | 1 (13) | 14 (9.8) | 4 (3) | 3 (2.5) | 4 (2.5) | 8 (8) | 4 (4) | 3 (2) |
| | Low | M | 64 | 13 (12.5) | 12.5 (12.5) | 22.5 (13) | 10 (9.8) | 1 (3) | 4 (2.5) | 4 (2.50) | 8 (8) | 2 (4) | 1 (2) |
| D | High | F | 65 | 16 (15) | 2 (15.5) | 2 (15.5) | 15 (8.3) | 3 (3.2) | 4 (3.2) | 5 (3.3) | 18 (8.5) | 3 (5) | 1 (2) |
| | Low | F | 65 | 11 (15) | 25 (15.5) | 25 (15.5) | 5 (8.3) | 2 (3.2) | 4 (3.2) | 3 (3.3) | 4 (8.3) | 1 (5) | 4 (2) |

Note. Age = Months.

Three tasks (No-Reward, Difficult-Reward, Easy-Reward) = sum of ranks for Task Success with **lower scores corresponding better proficiency**

Teacher scores = a sum (out of 15) of the mean score across teachers; Peer proficiency, Popularity and Dominance = Sum of nominations by other children; Text in bold indicates anomalies to expected rankings

Main Experiment

Method

Participants

Eight children were used as models, four participants were excluded from the study due to experimenter error and the experiment was terminated early for three children as they seemed uncomfortable with continuing. The remaining 94 children (53 males) ranged from four years nine months to six years seven months ($M = 65.53$ months, $SD = 5.74$ months). There was no significant difference in the distribution of sex ($\chi^2(4, N = 94) = 0.55, p = .97$) or age ($F_{4, 89} = 0.30, p = .88$) across the five conditions.

Design

The High PPM and Low PPM were individually trained to remove a sticker from an ‘artificial fruit’ task using three alternative solutions that each included a sequence of causally irrelevant actions. Once each child was proficient s/he was video recorded completing the sequence of actions ending with the successful extraction of the sticker. Participants, initially, either interacted with this task (successfully extracting the sticker or not) or had no prior personal experience. They then watched the videos of the models retrieving the rewards using either a new solution or the same solution that the child had previously discovered.

Apparatus

The Sweep-Drawer-Lever Box (SDLB, see Figure 2) is a puzzle box that contains a reward held in place by a series of defences. Critically there are three separate solutions, a drawer, a sweep and a lever mechanism, that can be used to release

the reward. The SDLB is transparent with an opening at the top where a capsule containing a sticker can be inserted. The capsule falls on to an opaque green mid-level platform where one of three spatially separated, and functionally unique, pieces of apparatus can be manipulated in order to push the capsule from the mid-level to a lower level. These three pieces of apparatus are, (1) a silver sweep with a red handle that moves the capsule to a hole through which the capsule falls to the lower level, (2) a silver lever used to push the capsule to a hole causing it to fall to the lower level, and (3) a blue drawer upon which the capsules sits and by pulling the drawer handle, a gap is produced through which the capsule falls to the lower level. These solutions can also be used in combination and therefore there are seven possible solutions: Sweep, Drawer, Lever, Sweep-Drawer, Drawer-Lever, Lever-Sweep and Drawer-Sweep-Lever, the latter four of these will be termed ‘combination-solutions’. On the lower level the capsule rests behind a black opaque door which can be slid to the side to remove the capsule.

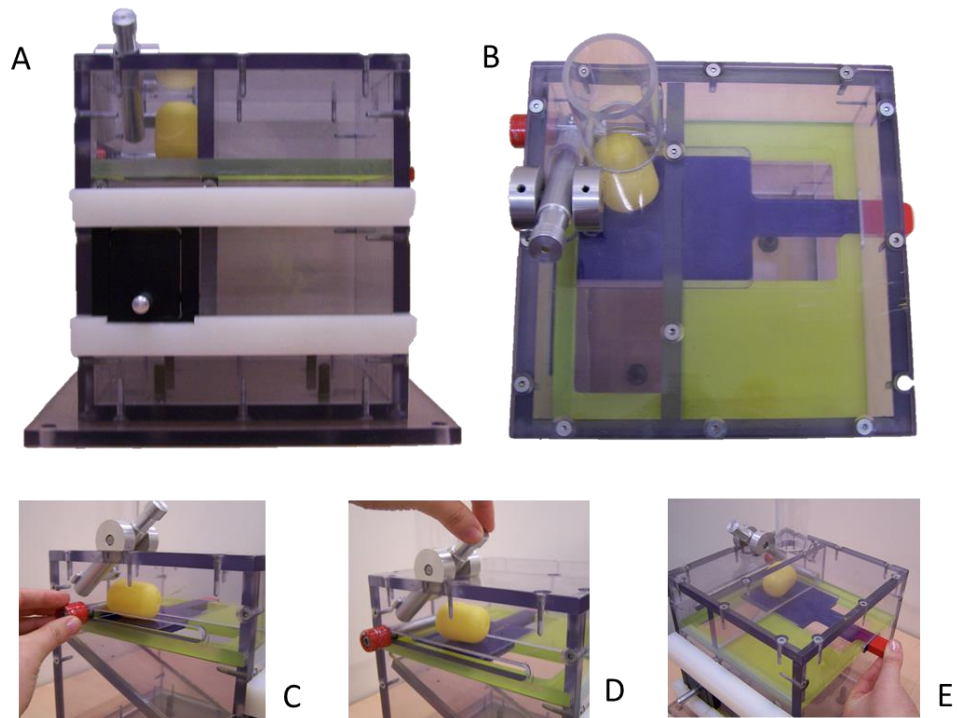


Figure 2. The Sweep-Drawer-Lever Box front view (panel A) and top view (B). Model using the sweep (C), the lever (D) and the drawer (E).

Video Demonstrations

The demonstrations were presented on two laptops, positioned on a table approximately 30cm apart. Children were initially shown three-second introductory clips of the models, one model for each laptop, smiling and waving. To aid the child's recall of which model would be shown on which laptop, at the top of each laptop was a photograph (3cm x 5cm) of the corresponding model. Whether the High PPM or Low PPM model was presented on the left or right was counterbalanced along with the order of presentation of the introductory clips. The subsequent clips of the models demonstrating their task solution were 15s long and were shown simultaneously. A video camera was placed 60cm in front of the participant so that his/her head and eye orientation towards the two laptops could be recorded.

Table 5: Overview of the procedure (three phases) in the five conditions

| | 1 | 2 | 3 | 4 | 5 |
|---|------------------------------------|-----------------------------|---------------------------------|---|--|
| Condition | None-then- two-alternate | Fail-then-two- alternate | Personal-then- two-alternate | Personal-then- High-PPM-same- Low-PPM- alternate | Personal-then- Low PPM-same- High-PPM-alternate |
| Phase 1 (Participant's interaction) | No interaction | Fail | Succeed | Succeed | Succeed |
| Phase 2 (Models' demonstrations) | Two new solutions | Two new solutions | Two new solutions | High same solution Low new solution | High new solution Low same solution |
| Phase 3 (Participant's interaction) | Six Trials | Six Trials | Six Trials | Six Trials | Six Trials |
| N | 20 | 12 | 21 | 20 | 21 |

Note: Words in bold font represent abbreviated terms, used in the text, for condition names.

Procedure

Children were tested individually in a quiet place in their school. The experiment consisted of three phases, and participants were systematically allocated to one of five conditions (see Table 5). In Phase 1 children were given either a chance to interact with the SDLB or were given no information. Children given no information (condition 1, Table 5) moved straight into Phase 2 where participants watched the introductory clips of the models. They were asked to identify the models by name, after which they received a demonstration of one solution from the High PPM and one from the Low PPM simultaneously. The demonstrations were repeated for a second time, again simultaneously.

Children who were assigned to the conditions involving an initial interaction with the SDLB were given one response trial (Phase 1); children could successfully extract the reward using the sweep, drawer or lever solution or fail to extract the reward. Those who were unsuccessful received a demonstration of one solution from the High PPM and one from the Low PPM (condition 2). Those who were successful were given one of three demonstration combinations: a demonstration of one solution from the High PPM and one from the Low PPM, both of which were different from the child's Phase 1 solution (condition 3), a demonstration of the same solution the child had used by the High PPM and an alternative solution by the Low PPM (condition 4) or a demonstration of the same solution the child had used by the Low PPM and an alternative solution by the High PPM (condition 5). The solution a model type used was counterbalanced across all trials. A demonstration consisted of the clips being shown simultaneously and repeated a second time. All demonstrations contained irrelevant actions; after the child model had caused the sticker to fall to the lower level using one of the three manipulandi they moved this same manipulandi back and forth a further

five times. For example, if they demonstrated drawer they pulled the drawer out to release the capsule then pushed the drawer (1) in, (2) out, (3) in, (4) out and, (5) in.

In Phase 3 all children were told, “It’s your turn (again).” The child was allowed to interact with the SDLB until s/he retrieved the reward successfully or three minutes had elapsed. If children were successful they were told, “It’s your turn again,” until they had completed six trials. At the end of testing all children were told they had done very well and were rewarded with stickers, irrespective of their level of success.

Coding and Inter-Rater Reliability

Each participant’s performance was scored with regard to eye orientation during video demonstrations and three separate variables for each response trial: (a) success (sticker removal), (b) solution used, (c) number of irrelevant actions copied (out of five). The experimenter, LW, coded 100% of the sample from video tape. An independent observer coded 25% of the sample for 22 variables (the three variables listed above for each of six trials and four variables relating to eye orientation). There was almost perfect agreement (Viera & Garrett, 2005) on 21 of the 22 variables (Kappa scores above .86 ($p < .01$)). The remaining variable (the number of irrelevant actions on the final trial) had a Kappa score of .64. A second independent observer coded 100% of this variable with a Kappa score of .86 ($p < .01$). All statistical tests are non-parametric and two-tailed.

Results

In Phase 1, 62 (81%) of the 77 naïve children who initially interacted with the task were successful. One child used both the Sweep and the Lever action during his success. The other 61 children used a single solution: 19 used the Drawer, 12 the Sweep

and 30 the Lever. The higher incidence of using the Lever was significant ($\chi^2(2, N = 61) = 7.71, p < .05$). For all subsequent analysis Kruskal-Wallis tests were run to investigate whether the lever impacted upon results. At no point did the salience of the lever have a significant impact upon the children's subsequent behaviour ($ps > .05$).

Prior Experience and Solution Choice

We predicted that children who discovered a solution and subsequently observed new alternate solutions from the two models would try one of these alternate solutions on their first subsequent attempt, but ultimately incorporate all solutions into their repertoire. Twenty-one children who personally discovered one solution were subsequently shown two novel alternative solutions. In their first response trial (T1) eight children (38%) used the solution demonstrated by the High PPM, seven children (33%) used the solution demonstrated by the Low PPM, two children (9%) used the solution they had initially discovered and the remaining four children (18%) used a combination-solution. Therefore, children were significantly more likely to deviate from their original solution than to use it again ($p < .001$, Binomial test). As children also used combination-solutions, post-hoc comparisons were run to see whether Phase 1 experience (failure or none versus success) affected exploration beyond personal and socially demonstrated solutions. Children who were unsuccessful in Phase 1 (Fail-then-two-alternate) were less likely to explore (use a solution not seen previously) the task than children who had been successful in Phase 1 (Personal-then-two-alternate, Fisher's Exact test, two tailed, $p < .05$). This was investigated further by comparing how many varieties of solutions (from seven possibilities) children used in their six response trials *that they hadn't used in Phase 1*. Corrected Mann-Whitney pairwise comparisons indicated that, even discounting the use of the solution acquired in phase 1, children in

the Personal-then-two-alternate condition used significantly more solutions in Phase 2 ($M = 2.29$, $SD = 0.64$) than children in the Fail-then-two-alternate condition ($M = 1.08$, $SD = 0.67$; $Z_2 = -3.83$, $p < .001$). There were no significant differences between the number of new solutions used for children in the Personal-then-two-alternate condition and the None-then-two-alternate condition ($Z_2 = -3.83$, $p = .73$).

We also predicted that children with successful prior personal experience would copy significantly fewer irrelevant actions than children with unsuccessful or no prior experience. There were no significant differences in the total number of irrelevant actions across the five conditions (Kruskal-Wallis, $N = 94$, $p = .59$). For those 77 children who had an initial successful interaction with the task, 12 (19%) performed an irrelevant action; two performed five or more (on the Lever and Sweep-Lever combination), two performed two, and eight performed a single irrelevant action, as though ‘tidying up’ (putting the manipulandi back in to its original position). Thus, the baseline for the rate of spontaneous irrelevant action production with the SDLB was 19% of children. Across all conditions, after social information (containing the demonstration of irrelevant actions), there was no increase in the proportion of children producing an irrelevant action. The only exception to this low frequency of irrelevant action production was for children who were initially unsuccessful, where seven of the ten (70%) subsequently successful children performed an irrelevant action on at least one trial; however the small sample size of this group negates statistical interpretation.

Past-proficiency Model-Based Biases

Across all conditions there were 39 children who used the High PPM solution, 38 who used the Low PPM solution which was not significantly different (Binomial, $p = .60$), 15 children used an alternative solution and two children were unsuccessful.

Across all six trials there was no significant difference in the number of times the High PPM solution ($M = 2.02$, $SD = 2.15$) or Low PPM solution was used ($M = 2.29$, $SD = 2.01$, *Wilcoxon* $Z = -0.70$, $p = .48$). This section focusses on our prediction that naïve children (no prior success) who observe differing solutions from two models will preferentially copy the solution choice of the High PPM over the Low PPM. We looked at this across two conditions:

Children with no initial experience (condition 1). Eighteen of the 20 children that had no prior interaction with the task before witnessing a demonstration went on to be successful at retrieving the reward from the task following a demonstration. Two children were unable to identify both models, one of these was unsuccessful and the other child was successful and used all three solutions in his trials. Of the remaining seventeen children, six children used the same solution as the High PPM, 11 children used the same solution as the Low PPM and no children used an alternative solution in their first trial (T1). There was no significant difference in whether the High or Low PPM's solution was used in T1 ($p = .33$, Binomial test, $\Theta = .31$). Over the six response trials there were no significant differences between the number of times the children used the High ($M = 1.88$, $SD = 2.23$) and the Low ($M = 3.24$, $SD = 2.17$) PPM's solution (*Wilcoxon* $Z = -1.35$, $p = .18$, $\Theta = .94$, see Figure 3). During T1 to T6, five children used a solution different to the two demonstrated; two used a single solution, one a combination-solution and two used both a previously unseen solution and a combination-solution on different trials.

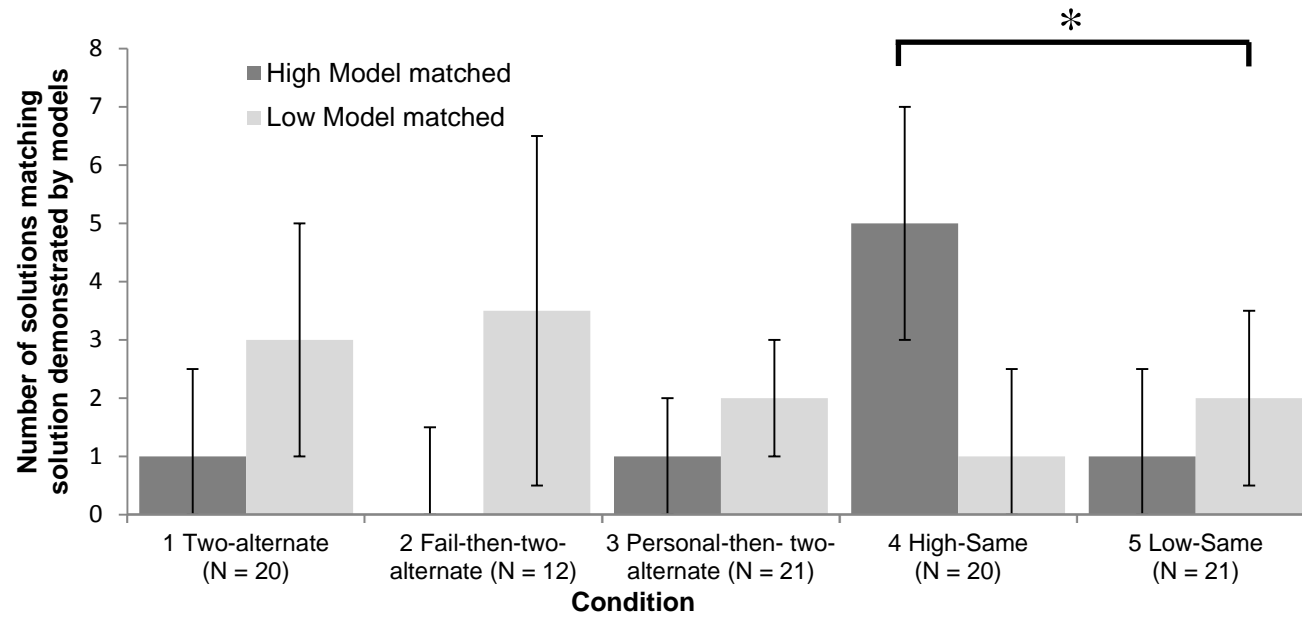


Figure 3: Median and interquartile range of mean number of respective solutions used across the six trials in Phase 2.

Children who were initially unsuccessful (condition 2). The 12 children who were unsuccessful at Phase 1 were given two different demonstrations, one from each model. As the small sample negates meaningful statistical analysis, the children's behaviour will be described. Ten of the 12 children (83%) went on to be successful following a demonstration. Every child used one of the two solutions demonstrated and no child used a third or combination-solution. In their first trial (T1) three children used the solution demonstrated by the High PPM and seven used that demonstrated by the Low PPM. Seven children (one who used the High PPM solution in T1 and six who used Low solution in T1) continued to use the same solution for all remaining trials (T2 to T6, see Figure 3). Conversely, three children (two who originally used the High PPM solution and one child who originally used the Low PPM solution) tried both solutions witnessed at some point in their trials (T1 to T6).

Section Three: Interaction between Personal Experience and Past-proficiency:

We predicted that children who discovered one solution and who witnessed two alternatives would preferentially copy the solution choice of the High PPM over the solution of the Low PPM. On their first attempt in Phase 3 there was no significant difference between whether a child used the High PPM's solution, the Low PPM's solution or their original solution ($\chi^2(2, N = 21) = 0.29, p = .87, \Theta = .89$). Over all trials (T1 to T6) there was no significant difference between the number of times children used the High PPM's solution ($M = 1.29, SD = 1.49$), the Low PPM's solution ($M = 2.10, SD = 1.67$) and their original solution ($M = 2.00, SD = 1.30$, Friedman's $\chi^2(2, N = 21) = 2.72, p = .26, \Theta = .99$, see Figure 3). Seven (33%) children used combination-solutions at some point during the six trials.

We also predicted that children who discovered a solution and subsequently observed one personal-matching and one novel solution would be more likely to attempt an alternative if that alternative is demonstrated by a High PPM versus Low PPM. Forty-one children discovered a solution at Phase 1 and subsequently observed one model using the same solution they had discovered and one model demonstrating a novel alternative. Twenty children witnessed the Low PPM match their solution choice and a High PPM demonstrate a new solution. In T1 these children were more likely to try a new solution ($N = 15$) than use their original (and Low PPM matching) solution ($N = 5$, Binomial, $p < .05$). However, six of these children discovered an alternative solution. Twenty-one children witnessed the High PPM match the child's solution and Low PPM demonstrates an alternative. These children were not more likely to use a new solution ($N = 9$; Low = 8, Alternative = 1) than use their original (and High PPM matching) solution ($N = 12$, Binomial, $p = .66$). The difference between the two conditions in terms of repeating their own solution approached significance ($p = .058$, Fisher's exact, two tailed). Throughout the remaining trials (T2-6), children in the High-same-and-Low-alternate condition continued to use their original solution ($M = 3.89$, $SD = 2.22$) more frequently than children in the Low-same-High-alternate condition (see Figure 3, $M = 2.00$, $SD = 1.89$; $Z_2 = -2.49$, $p < .05$). Not only were children in the Low-same-High-alternate condition more likely to deviate away from their originally discovered solution to that demonstrated by the High PPM, but they were significantly more likely to find the third, undemonstrated, solution than children in the High-same-and-Low-alternate condition ($\chi^2(1, N = 41) = 7.55$, $p < .01$).

Section 4: Post-hoc Analysis of Children's Attendance to the Demonstrations

During the demonstration phase children had a choice as to which model they watched. Children's head and eye movements were recorded and coded both for the number of times and total duration that each demonstration was attended to. On the first demonstration 49 children (53%) looked at the High PPM initially and the remaining 44 children looked at the Low PPM. On the second demonstration 43 children (46%) looked at the High model and the remaining 50 children looked at the Low PPM initially. The majority of children alternated their attendance between the two screens during each demonstration (head direction changes between laptops, $M = 4.6$, $SD = 2.4$). In the first and second demonstration only nine (10%) and ten (11%) children watched the High PPM exclusively and four (4%) and twelve (13%) children the Low PPM exclusively. A mixed-model ANOVA with Condition ($N = 5$) as the between subjects factor and Demonstration number ($N = 2$) as the within subjects factor showed no main effect of Condition ($F_{4,87} = 0.36$, $p = .84$), no main effect of Demonstration number ($F_{1,87} = 0.71$, $p = .40$), and no interactions between Demonstration and Condition ($F_{4,87} = 0.20$, $p = .94$) upon the time spent looking at the High PPM (and therefore conversely the Low PPM) during the demonstration phase. In order to test whether the children's attendance during the observation phase affected their subsequent behaviour, the dependent variable of which model's solution (High PPM or Low PPM) was used in the children's first response trial (Phase 3) was entered separately into a stepwise binary logistic regression along with which model was attended to first (High PPM or Low PPM) and cumulative duration of attendance to each model in both demonstration phases. The only significant predictor of Phase 3 behaviour was which model was attended to first ($\beta = -1.11$, $p < .05$). Across all conditions, if the High PPM was attended to first, the child was significantly more likely to use the High PPM's solution

first, and if the Low PPM was attended to first, the child was significantly more likely to use the Low PPM's solution first.

Discussion

Before reflecting on the main results we briefly discuss the model selection data. This study enabled children to gain personal experience with a task, before they witnessed familiar others of differing proficiency use the task. There was evidence that our novel tasks were able to appropriately assess the proficiency of the children. Additionally, the teacher's predictive ratings of proficiency correlated with the two reward-related tasks suggesting that the tasks appropriately elicited the traits considered by the teachers to assess proficiency. These traits were originally developed for chimpanzees and were rated by care staff (Freeman et al., submitted) where they also appeared to map onto a single construct and ratings were highly consistent across husbandry staff. In accordance with other studies (Pellegrini et al., 2007), teacher ratings of characteristics reliably predicted the success of children with the novel tasks.

Children's ratings of proficiency were inconsistent as they failed to reliably pick the same peers twice for the same trait. Furthermore their ratings did not correlate with the children's behaviour on the two reward-related tasks. However, the fact that children showed a past-proficiency model-based bias under certain test conditions indicates that they do have the ability to discern between models of varying historical ability and use this to guide their behaviour. Therefore, it could be that the current study's methods of asking the children who would be good at a novel task were not appropriate.

Alternatively, it is possible that other model-based biases overshadowed a past-proficiency bias; children preferentially selected older, more popular peers of the same sex in their proficiency ratings. Indeed, in another study, of equivalently aged children,

children's imitative behaviour was more influenced by a model's age over a model's knowledge state (Wood et al., 2012). In the current study, once models were matched on potential model-biases beyond PPM (e.g., age, sex, popularity and dominance) children's behaviour in the main experiment was affected by a past-proficiency model-based bias under conditions where one model matched the child and one model offered an alternative. There are a multitude of model characteristics that might elicit model-based biases; implementing some biases will be cognitively demanding and the some characteristics that bias will be more subtle. There may also be a developmental shift with regard to how and when different model characteristics are perceived and used to bias children's learning (Wood et al., submitted).

Solution Choice

Children with no prior interaction with the task showed canalisation in their behaviour following demonstrations from the two models; these children failed to discover solutions beyond those demonstrated. Previous research has demonstrated that children who have a difficult task experience are significantly more likely to faithfully imitate modelled solutions (Williamson & Meltzoff, 2011). In contrast, children who discovered a solution for themselves and subsequently observed new alternate solutions, employed by the two models, tried these alternate solutions, ultimately incorporating all solutions into their repertoire and discovering additional combination-solutions. This finding corresponds to an earlier result using a simpler version of the SDLB (without the lever) where personal experience prior to receiving a social demonstration, increased solution discovery (Wood et al., in press). A motivation to incorporate new solutions into one's repertoire appears in previous research, including those in different domains (Siegler & Opfer, 1996) indicating that children's acquisition of multiple solutions is

beneficial to learning about the specific task and to more general forms of learning.

Learning new solutions may assist adaption in a changing environment (Inglis et al., 1997) and therefore is an adaptive strategy.

Generally, children did not imitate the irrelevant actions which stands in contrast to a number of studies showing that children around this age faithfully reproduce irrelevant actions (Horner & Whiten, 2005; Lyons, Young, & Keil, 2007; McGuigan et al., 2007). The irrelevant action reproduction seemed to be close to ‘floor’ levels and this may well be why there were no group differences. The only condition that showed a pattern towards irrelevant action reproduction was for those children who were unsuccessful during their original attempt. This pattern mirrors Williamson and Meltzoff (2011) who showed that a difficult, versus easy, prior experience increased the chances of irrelevant action reproduction. Our work does support previous research that has shown minimal copying of casually irrelevant actions when the model is a child (Wood et al., 2012) and the demonstrations were via video rather than live (McGuigan et al., 2007). We also believe that the viewing of two demonstrations simultaneously may have increased the cognitive load and thus decreased the fidelity of copying a model’s solution. However, although the conditions of the current study may have been cognitively demanding, the children did still show imitation of the relevant actions. This selective imitation of relevant but not irrelevant actions could imply that children understand what is causally relevant and what is not and when a copying context is difficult will focus on functional and parse out non-functional aspects.

Past-proficiency Model-based Biases

Our prediction, that naïve children who observe differing solutions from two models will preferentially copy the solution choice of the High PPM over the Low PPM

was not supported. Whilst this stands in contrast to other studies where children have shown model-based biases for past-proficiency (Koenig & Harris, 2005b), our study had a different methodology; both demonstrations offered a viable solution. Therefore, we suggest that a failure to show a model-based bias may be due to children's motivation to try any new success, irrespective of the source of that success. A similar pattern of behaviour has been found previously whereby functionally relevant solutions were imitated regardless of model characteristics (age/knowledge state) yet the reproduction of demonstrated irrelevant actions was affected by model age (Wood et al., 2012). If one has no prior information a model's characteristics may be important when one has to discern which solution offered is viable or what actions within a solution are relevant but if both models offer a viable solution their characteristics may not influence one's solution choice.

Interaction between Past-proficiency Bias and Solution Choice

There was some evidence of a past-proficiency model-based bias; when the High PPM matched the child's original solution the child was more likely to continue using this solution than when the Low PPM matched the child's solution. When the Low PPM matched the child's original solution, children were as likely to employ the High PPM's solution as continue using their own and they also discovered more previously unseen solutions as compared to the group who had the High PPM match. A preference for information provided by a High PPM has been shown in studies where models offer differing answers but only one is 'correct' (e.g. calling a ball 'a horse' Birch et al., 2008; Koenig et al., 2004; Koenig & Harris, 2005b; or putting shoes on hands rather than feet Zmyj et al., 2010) and has also been tentatively indicated in

human's closest living ancestor, chimpanzees (Horner et al., 2010; Kendal et al., in prep).

In contrast to those who have no prior success, if a child is successful it may be beneficial to evaluate their own and alternative methods and model characteristics may guide this. This would indicate that selectivity based on a model's past proficiency may only be important when the observer is less concerned about acquiring any information that might lead to success but more concerned with assessing their solution and the task as a whole.

We suggest that when the child and High PPM' solutions match, that solution is established as a 'good solution' and will increase fidelity towards this solution over time. Conversely, when the child and Low PPM agree but the High PPM provides an alternate solution, the child perceives that his/her solution (and Low PPM's solution) is only one of many ways to interact with this task and uses the High PPM's solution as well as exploring the task.

Attendance to Demonstrations

There was no discernible pattern regarding attendance to models during demonstrations. However, on their first attempt children were significantly more likely to use the solution of the model they had attended to first. This would suggest one of two things; that children decide who they would like to observe, and potentially copy, before the start of the demonstrations or that children's choice of who to observe first is random but this choice influences whom they subsequently copy. This latter explanation may represent a primacy effect which could be explored if there were conditions where children were told who to look at first or if model demonstrations were played sequentially rather than simultaneously.

Conclusion

The current study investigated whether children's solution choice of a tool-use task was influenced by continued experience and the past-proficiency of a model. Children were motivated to incorporate asocially learned and socially demonstrated task solutions into their repertoire. When both models offered previously unseen and viable solutions, this motivation to acquire solutions seemed to be more salient than the characteristics of the models who demonstrated them. However, when certain familiar peers matched a child's solution and other familiar peers offered an alternative, children's continuation of their own solution was influenced by the past-proficiency of those peers. Children's solution choices demonstrate the complex nature of children's social learning strategies. Even at this young age, children's learning is sophisticated in that they are able to remember and successfully use a number of quite different solutions on a single task and they seem able to track and appraise the past behaviour of familiar peers, compare these individuals; "A is more proficient than B", and then use this to guide their behaviour. Children's solution choices also seem adaptive because it potentially results in the social transmission of the most useful information, the extensive accumulation of knowledge, and iterative improvements in task interaction, over time which is thought to underpin our species unique capability for cumulative culture (Boyd & Richerson, 1985). Children's social learning is complex and needs to be viewed in a dynamic setting considering personal experience, number of solutions available, models and demonstrations witnessed.

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Chapter VI

Chimpanzees' tool-use is biased by the proficiency of known conspecifics

This final empirical study built upon the research presented in the previous study. Past-proficiency model-biases in captive chimpanzees were investigated with an adapted design. Specifically, chimpanzees learning of a tool-use task, relative to the past-proficiency of known conspecifics (group mates), was investigated. It is anticipated that the data presented in this chapter, will be submitted for publication either in a journal specialising in animal behaviour or one with a more general readership relating to cultural evolution. The authorship would be as follows: Lara A. Wood¹, Rachel L. Kendal², Lydia M Hopper³, Susan, P Lambeth⁴, Steven, S Schapiro⁴ and Emma G. Flynn¹

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Abstract

There is still much debate over the learning processes and transmission biases underpinning chimpanzees' social learning. The current study employed a novel tool-use paradigm in an open-diffusion setting to investigate these factors. Within their groups, chimpanzees had access to pairs of visually and functionally different tools (hook and scoop) which could be used to obtain baskets containing food. Chimpanzees either had no prior information regarding the task or received demonstrations from two models, each demonstrating a different tool. These two models differed in their prior-proficiency as ascertained by prior interactions with novel tasks (that other group members observed, so potentially developing a within group proficiency reputation) and husbandry employees' ratings of each chimpanzee's general proficiency. There were no significant differences in success rates in the use of tools by chimpanzees from the model-groups and groups in which there were no models. However, the first tool touched by chimpanzees from the model-groups indicated a model-based transmission bias as individuals were significantly more likely to match the tool demonstrated by the model with the higher past proficiency than the lower past proficiency. The tool used for chimpanzees' first attempts and first successes did not differ as a function of which model used the tool. It is proposed that chimpanzees' tool-use behaviour was guided by an initial bias towards the model with higher past proficiency, alongside asocial learning. The majority of chimpanzees used both tools and some asocially learned new methods of reward retrieval.

Introduction

Chimpanzees socially learn. That is, chimpanzees observe others and this influences their interactions with their environment. For example, chimpanzees are more likely to obtain out of reach food with a tool after a social demonstration of that tool than with no information (Nagell, Olguin & Tomasello, 1993; Tomasello, Davis-Dasilva, Camak & Bard, 1987). More broadly, the ability to socially learn is thought to underpin the spread of different behavioural patterns in varying locations in the wild; hence it underpins culture in chimpanzees (Whiten et al., 1999). Despite these studies, what chimpanzees learn, i.e. the processes and mechanisms of the transmission of social information, is still a matter of some debate (see Whiten, Horner, Litchfield, & Marshall-Pescini, 2004 and Hoppitt & Laland, 2008 for a detailed description of social learning processes and mechanisms). Here mechanisms refer to the outcomes of the social learning rather than the cognitive mechanisms underpinning these outcomes (Heyes, 2012).

Matthews, Paukner and Suomi (2010) propose that simple social learning mechanisms, such as stimulus enhancement, combined with asocial learning and reinforcement can result in behavioural traditions. Stimulus enhancement is a relatively rudimentary learning mechanism, defined as an increase in the probability that the observer will interact with stimuli of the same physical type as those with which the demonstrator interacts (Heyes, 1994). Stimulus enhancement alone cannot explain all forms of chimpanzee learning; Nagell et al. (1993) found that, whilst chimpanzees who observed no demonstrations were as likely to manipulate a target tool as those who observed a conspecific demonstration, the no-demonstration chimpanzees were less likely to successfully obtain a reward. The chimpanzees with a social demonstration did not imitate the precise two-action step of the model, suggesting an absence of

behavioural imitation but a presence of end-state emulation. Accordingly, it has been suggested that chimpanzees are more ‘goal emulators’ than ‘action imitators’ (Whiten, McGuigan, Marshall-Pescini & Hopper, 2009). In other circumstances chimpanzees copied the exact actions employed by models during reward retrieval (Whiten, Custance, Gomez, Teixidor & Bard, 1996; Whiten, Horner & de Waal, 2005; Whiten et al., 2007) but they do not do so with the same fidelity as children (Call, Carpenter & Tomasello, 2005; Nagell et al., 1993; Whiten et al., 1996). This plethora of research demonstrates that different paradigms might elicit different learning mechanisms and that chimpanzees might employ ‘a portfolio of alternative social-learning processes in flexibly adaptive ways, in conjunction with nonsocial learning’ (Whiten, et al., 2004, p. 36).

The current research investigated social transmission of information using a novel design; two tools, a scoop tool and a hook tool were made available to chimpanzees. Each tool entailed its own method (hooking with the hook or scooping with the scoop) of obtaining an out-of-reach basket containing food. Chimpanzees either received no prior demonstrations of basket retrieval or received demonstrations from two models, each model demonstrating the use of just one of the tools. By using known conspecifics as models, the aim of the current study was to implement an experimental design which mirrored captive chimpanzees’ naturalistic settings. These known conspecific models differed in their past proficiency as potentially ascertained by group members due to (1) prior interactions with novel tasks within the group context and (2) husbandry employees’ ratings of each chimpanzee’s general non-social proficiency as observed over a period of at least 18 months. Ecological validity was increased by implementing an open-diffusion design whereby the models demonstrated to the whole group and subsequently the task was made available to the whole group

(Whiten et al., 2007). It is argued that diffusion experiments allow for greater experimental validity because they allow investigation of how behavioural variations spread and how faithfully they do so (Mesoudi & Whiten, 2008; Whiten & Mesoudi, 2008). The following two sections discuss model-based-biases and solution (or tool) choice in this context.

Model-based Biases

It has been proposed that animals use heuristics to guide when, and from whom, they socially learn. These social learning strategies (Laland, 2004) may be influenced by the characteristics or the behaviour of the model demonstrating the behaviour. Henrich and Gil-White (2001) argue that ‘Natural selection favoured social learners who could evaluate potential models and copy the most successful among them’ (p. 165). Such strategies have been termed context-dependent model-based biases (Boyd & Richerson 1985; Henrich & McElreath, 2003; Rendell et al., 2011). There have been theoretical models of the utility of a success bias (Baldini, 2012) but there is limited empirical work investigating model-based biases in chimpanzees. Wild chimpanzees show selective attention towards observing models of the same age or older, but not younger, than themselves (Biro, Inoue-Nakamura, Tonooka, Yamakoshi, Sousa, & Matsuzawa, 2003), and captive chimpanzees’ learning of food retrieval methods is influenced more by older versus younger individuals (although the older chimpanzees were also more dominant and were rated as having higher past proficiency by husbandry staff (Horner, Proctor, Bonnie, Whiten, & de Waal, 2010). Dominance may also affect learning as behaviour demonstrated by a subordinate chimpanzee is not socially learned (Bonnie, Horner, Whiten, & de Waal, 2007) and that there is an ‘attendance bias’ towards dominant chimpanzees for learning purposes (Kendal et al., in prep.).

The focus of this study was the model-based bias of success. Rendell et al., (2011) identify three ways in which model success might bias learning. Individuals might copy: (1) in proportion to observed payoffs, (2) if a model's payoff is better than their own, and (3) the model thought to be the most successful. However, it is unclear whether model success relates to the present, i.e. the model is successful at demonstrating the information which may be transmitted, or in the past i.e. that the success was demonstrated in the past and that some form of 'success reputation' is biasing subsequent information transmission from model to observer. Furthermore, it is not clear whether success relates to domain specific model success relating to the specific information which is to be transferred or whether it is domain general success i.e. that the model generally has more success in their environment which may also be related to dominance and prestige (Henrich & McElreath, 2003).

Therefore, as stated earlier, we use the term past-proficiency to refer to a model's domain-specific ability shown in the past. As such it focusses on the potential for a model to have a reputation for being skilled within the domain in which the model is currently demonstrating. A bias towards those who have shown themselves to be previously proficient in the same domain as the to-be-learned task requires an ability to track other's behaviour over time and, with regard to that individual, adapt one's behaviour accordingly. This has been demonstrated with chimpanzees that develop a preference for gesturing to a long-term generous versus ungenerous donor (Subiaul, Vonk, Okamoto-Barth & Barth, 2008). A proficiency bias also requires that chimpanzees are able to identify a model's characteristics and use these to guide their copying. As mentioned above, there is evidence that chimpanzees are able to use such characteristics as they preferentially copy the choices of older, higher ranking and previously proficient models (Horner et al., 2010). However, it is not known whether it

was the age, dominance and/or prior proficiency which influenced the chimpanzees' choices and the study had a limited sample size. Across species, children show a bias towards a model with a higher, rather than lower, past proficiency both with novel word learning (Koenig & Harris, 2005b; Vázquez, Delisle, & Saylor, 2012) and artefact use (Birch, Vauthier, & Bloom, 2008; Zmyj, Buttelmann, Carpenter & Daum, 2010). In an artefact design task, human adults also use a 'copy successful' bias when the task is relatively hard (Mesoudi, 2008) but in a lower than expected frequency (Mesoudi, 2011) and it is used to the same degree as a prestige bias which was contextually less useful (Atkisson, O'Brien & Mesoudi, 2012).

In the current study we investigated whether chimpanzees' behaviour was influenced by a model-based bias pertaining to known conspecifics' previous proficiency. Prior-proficiency in this context related to proficiency with novel tasks which were similar to the test-task leading to a prior-proficiency construct in the domain of food retrieval. Chimpanzees had spent a minimum of 18 months in their groups and some chimpanzees had spent up to 36 years in each other's company. This sustained amount of group living and the opportunity to witness conspecifics interacting with novel tasks in the same domain as the test-task meant there was potential for chimpanzees to perceive the proficiency of others. Within each experimental group a chimpanzee ranked as having a higher past proficiency was chosen as a model (High PPM) along with a chimpanzee ranked as having a neutral-to-low past proficiency (Low PPM). These chimpanzees were trained to use one of two distinct tools to retrieve food. Once the two models were proficient, they demonstrated their tool use to the group and subsequently two sets of tools were made available to the whole group. We predicted that chimpanzees who observed differing solutions from two models would initially copy the solution choice of the High PPM.

Solution Choice over Time

It has been proposed that chimpanzees who discover, or socially learn, one solution for food retrieval are unlikely to try a more efficient solution (Marshall-Pescini & Whiten, 2008) and when one solution is precluded, those expert in the blocked solution do not adopt an alternative solution (Hrubesch, Preuschoft, & van Schaik, 2009). Similarly, Hopper, Schapiro, Lambeth and Brosnan (2011) found conservatism to initial social information even when an equally-easy alternative behaviour produced a higher value reward. However, chimpanzees in the wild exhibit flexibility in using a range of tools for food acquisition such as obtaining honey (Sanz & Morgan, 2007, 2009) although the extent to which each tool is fixed for use for each stage of the extraction process is unknown. Captive chimpanzees, that asocially learn one technique for obtaining juice, permanently switched to using a more efficient technique upon observing a conspecific or human demonstrate this more proficient alternative (Yamamoto, Humle & Tanaka, 2013) and Dean, Kendal, Schapiro, Thierrey, and Laland (2012) found no conservatism to initially rewarded solutions when greater rewards were obtainable. This suggests that solution change can occur with sufficiently persuasive social information. Additionally, Hopper, Spiteri, Lambeth, Schapiro, Horner and Whiten (2007) found that when chimpanzees received a demonstration of a difficult method of reward retrieval they adopted the alternative method available, indicating that costs to using an original method might result in solution switching as has been found in other species involving prior personal and subsequent social information (see Kendal, Coolen, van Bergen, & Laland, 2005 for a review). In apparent contrast to non-humans (Kendal et al. 2005), Wood, Kendal and Flynn (2013) found that, even when their

original personally-acquired information was sufficient, children attempted novel socially-demonstrated solutions and incorporated both solutions over time.

The current study extends previous research by introducing, or ‘seeding’, two socially demonstrated solutions before any observer interactions. The chimpanzees can choose which solution to attempt first and whether to incorporate both solutions. Due to this novel paradigm we make no specific predictions concerning whether the chimpanzees will demonstrate canalisation to the first method adopted or attempt both methods.

Summary

The current study investigated social transmission of information using a novel task design to investigate social learning processes and mechanisms, past-proficiency model-based biases and task interaction over time. Chimpanzees’ proficiency was assessed through observations of interactions with tasks that were similar to the test task. The potential for group-members to construct a proficiency reputation occurred during these group interactions. In addition proficiency rankings of husbandry staff were collected, leading to the selection of two proficiency contrasting models in four groups. This model selection procedure was rigorous, thus we present a concise method and results, followed by the method and results for the main model-based bias experiment.

Model Selection: Method

Subjects

The study included six groups totalling 54 chimpanzees (24 males) housed in six social groups at the Michale E. Keeling Center for Comparative Medicine and Research

of the University of Texas MD Anderson Cancer Center, Bastrop, TX, U.S.A.

(KCCMR). Subjects were aged 12- to 43-years-old ($M = 24.5$ years, $SD = 7$). The group sizes were as follows: A = 8 (4 males), B = 8 (3 males), C = 9 (6 males), D = 7 (4 males), E = 11 (2 males) and F = 10 (4 males). The chimpanzees were not deprived of food or water. Approval for this study was gained from the Institutional Animal Care and Use Committee of the University of Texas. The KCCMR is fully accredited by the American Association for the Accreditation of Laboratory Animal Care-International.

Apparatus

Four novel tasks were used: (1) Hard-Reward (rewards= food), (2) Easy-Reward, (3) No-Reward tube and (4) No-Reward mirror (see Figures 1a to 1d). Two tasks contained food, and two did not (see Clark and Smith, 2012 for evidence that task interactions do not decrease in the absence of food rewards).



Figure 1a: Easy-Reward task. 150cm Perspex pipe with a larger hole (diameter = 10cm) at one end and 12 smaller holes ($d = 3\text{cm}$) throughout the rest of the pipe. The pipe was filled with chow and apple pieces. Small pieces of food could be removed from the smaller holes or larger pieces of food could be moved through the pipe and removed from the larger hole.



Figure 1b: Hard-Reward task. 25cm x 25cm x 5cm (h x w x d) clear Perspex box with six compartments containing cereal. Each compartment had a hole ($d = 3\text{cm}$) at the front. On the front of the box was a circular clear disk with three holes ($d = 3\text{cm}$). This circular panel was attached with a bolt in the centre such that the panel could rotate. When a hole on the panel lined up with a hole on the box, food could be accessed.



Figure 1c: No-Reward tube task. 100cm clear Perspex pipe filled with 12 balls of differing colours, sizes and textures. The pipe had three slats cut into it ($l=10\text{cm}$, $h=2\text{cm}$) so that balls could be touched but not be removed from the pipe.



Figure 1d: No-Reward mirror task. 40cm x 40cm x 15cm ($h \times w \times d$) blue crate with a mirror attached to the front panel. The mirror has three holes cut into it through which chimpanzees could touch, two rotatable paint rollers.

Behaviour Ratings

In four separate 60min sessions, each task was individually made available to all members of each chimpanzee group. A video camera was placed 2m away from the task and all behaviour occurring at the window, where the task was attached, was recorded and coded. The experimenter (LW) was present at all times and gave a running

commentary of behaviour to aid with coding. The videos were coded for each individual's latency to first approach to within 1m of the task (1), contact interaction whether with hand or mouth (2), first food reward extracted (3) and latency between first approach to first food reward (4). Additionally, the number of approaches (5), interactions (6), interactions resulting in food reward (7), types of different interactions (8), food rewards retrieved (9) and ratio of 'unsuccessful' to 'successful' interactions with food rewarded tasks were recorded (10). Finally, the cumulative time (in seconds) spent within a 1m radius of the task (11) and interacting with the task (12) was also recorded.

Chimpanzees were ranked, relative to other chimpanzees in their group, for each of these behaviours, and the ranks summed to give a total rank for each task, henceforth called 'Task Success'. A lower rank equated with more Task Success. Pearson rank correlations demonstrated that chimpanzees' behaviour showed consistency across three of the four tasks (see Table 1). A sum of all behavioural scores on each of the tasks was significantly correlated with each other task except the No-Reward mirror task did not correlate with the Hard-Reward task and the No-Reward tube task. Scores for the novel tasks were standardised from a scale of 0 to 10 so that each chimp had a rank score relative to his/her group size.

Table 1: Pearson correlations of summed scores on all behaviours on four novel tasks

| | Hard-Reward | Easy-Reward | No-Reward Tube | No-Reward Mirror |
|------------------|-------------|-------------|----------------|-------------------|
| Hard-Reward | — | .66*** | .52*** | .25 ^{ns} |
| Easy-Reward | | — | .65*** | .41* |
| No-Reward Tube | | | — | .26 ^{ns} |
| No-Reward Mirror | | | | — |

*Note. Bonferroni corrections for six comparisons * $p < .009$, *** $p < .001$*

Husbandry Employee Ratings

Husbandry employee (HE) ratings were collected as an alternative assessment of chimpanzee past proficiency with novel tasks. Three HEs (A, B and C) at the KCCMR facility, who have worked daily with the chimpanzees for at least 18 months, were asked to rate chimpanzees using a 7-point scale, with 7 being the high extreme. There were three traits pertaining to proficiency: Inquisitive, defined as, ‘Readily explores new situations and objects’; Intelligent, ‘Quick and accurate in judging and comprehending non-social situations’; and Inventive, ‘More likely than others to engage in novel behaviours, e.g. Using new devices or materials in the enclosure’. HEs were also asked to rate chimpanzees on three traits relating to dominance: Aggressive, ‘Often initiates fights or other menacing and agonistic encounters with other chimpanzees’; Affiliative, ‘Has affiliative bond with either a significant number of others and /or a small number of more powerful individuals’; Acquiring ability, ‘Is able to acquire and monopolise resources over other individuals’. All traits were based on constructs developed, and validated for use with chimpanzees, by Freeman et al. (submitted). The three HEs independently gave each chimpanzee similar ranks for each trait (Spearman rank p s < .01), highlighting internal reliability with the proposed construct of proficiency. The scores of Inquisitive and sum scores were correlated across HEs, but scores of Intelligent and Inventive were not correlated across HEs (Inventive approached significance for HE A’s scores with the other two HE, see Table 2). Ratings of the summed dominance traits are presented in the model selection table (Table 4).

Table 2 HE ratings of proficiency

| Inquisitive | | Intelligent | | Inventive | | Sum | |
|-------------|------|-------------|------|-----------|------|------|------|
| HE B | HE C | HE B | HE C | HE B | HE C | HE B | HE C |

| | | | | | | | | |
|------|--------|------|------|-------------------|-------------------|------------------|-------|-------|
| HE A | .44** | .34* | .01 | .25 ^{ns} | .28 ⁺ | .32 ⁺ | .33* | .41** |
| HE C | .47*** | - | -.05 | - | .26 ^{ns} | - | .36** | - |

Note. Bonferroni corrections ⁺ $p < .05$, * $p < .017$, ** $p < .01$, *** $p < .001$

Relation between Behaviour and HE Ratings

The rank scores of performance with the four novel tasks were standardised to a scale of 0 to 10 so that each chimp had a rank score relative to his/her group size. This enabled an assessment of the relation between HE ratings and behaviour with the novel tasks for all 54 chimpanzees. Chimpanzee ranks for response to each novel task (lower rank indicating better task performance) were separately entered as dependent variables into a linear regression with each HE score entered as independent variables (see Table 3). HE A's proficiency ratings were a significant predictor of chimpanzee behaviour for two tasks (Easy-Reward and No-Reward Tube) and approached significance for the No-Reward Mirror. HE B and C's proficiency ratings were not significant predictors for any of the tasks. HE C's score approached significance for the No-Reward Mirror task; the more proficient a chimpanzee was rated, the poorer their actual performance. Performance with the No-Reward mirror task had correlated least well with the other tasks, perhaps explaining this anomaly.

Selecting Models

Chimpanzees' behaviour over three of the four novel tasks was consistent, demonstrating that chimpanzees' novel task proficiency was consistent across contexts. This period of group task interaction prior to the main experiment also potentially served to cement any proficiency reputations that chimpanzees possessed. HE ratings of proficiency generally positively correlated with each other but only one HE member (A) was consistently reliable in predicting chimpanzee performance with the novel tasks.

We, therefore, prioritised behaviour with the four tasks for model selection but also considered HE ratings. The High PPM was chosen from chimpanzees who reached the following criteria: ranked in the top three chimpanzees for Task Success with at least three of the novel tasks and was ranked in the top three chimpanzees for HE proficiency rankings (Table 4). The Low PPM was chosen from chimpanzees who reached the following criteria: did not come in the top three chimpanzees for Task Success with any novel task and ranked in the bottom four chimpanzees for HE proficiency scores. There were four chimpanzee groups in which two models were selected. Selection criteria were met for three of the four groups for the High PPM. In the fourth group (D) the two chimpanzees who fulfilled the high PPM criteria refused to voluntarily separate from their group. Therefore a chimpanzee who was rated highest by HEs was selected. This chimpanzee had not performed as well as the other High PPMs with the tasks but he still performed better than other chimpanzees within his group. This chimpanzee had initially appeared to show neophobia to the experimenter (LW) during the novel task phase perhaps explaining his lack of task interaction. After additional training this model chimpanzee seemed comfortable with the experimenter, voluntarily separating from his group. All subsequent analysis was performed with the inclusion and exclusion of this group and results remained the same. Thus the analysis presented here includes all four groups. Selection criteria were met for three of the four groups for the Low PPM, but in the fourth group (C) the one chimpanzee who reached criteria refused to voluntarily separate from her group. Therefore a chimpanzee who was rated the least proficient by HEs was selected. This chimpanzee only came in the top three for the No-Reward Mirror task. There were no models in groups E and F. A summary of the characteristics of all models can be seen in Table 4.

Table 3: Linear Regression (Enter) for chimpanzee behaviour (ranks) on the four novel task

| | Easy-Reward | | | | Hard-Reward | | | | No-Reward Tube | | | | No-Reward Mirror | | | |
|-----------|---------------|-----|---------|-------|-------------|-----|---------|-------|----------------|-----|---------|-------|-------------------------|-----|---------|-------|
| | B | SE | β | t | B | SE | β | t | B | SE | β | t | B | SE | β | t |
| Husbandry | | | | | | | | | | | | | | | | |
| Employees | | | | | | | | | | | | | | | | |
| A | -.30** | .1 | -.42 | -2.24 | -.19 | .11 | -.26 | -1.73 | -.37*** | .10 | -.52 | -3.75 | -.25⁺ | .11 | -.34 | -2.32 |
| B | -.06 | .19 | -.05 | -0.32 | -.16 | .20 | -.11 | -0.77 | -.07 | .19 | -.05 | 0.35 | -.06 | .20 | -.04 | -.30 |
| C | .26 | .14 | .26 | 1.77 | .26 | .14 | 0.26 | 1.75 | .18 | .14 | .18 | 1.29 | .32⁺ | .15 | .32 | 2.19 |

Note. Bonferroni corrections for each of the four comparisons ⁺ $p < .05$, * $p < .012$, ** $p < .01$, *** $p < .001$

Table 4: Overview of the eight models, two selected from each group

| Group | Model | Sex | Age | Easy-Reward Converted Rank | Hard-Reward Converted Rank | No-Reward Tube Converted Rank | No-Reward Mirror Converted Rank | HE Proficiency Score (Group <i>M</i>) | HE Dominance Score (<i>M</i> = 4.1 <i>SD</i> =1) |
|-------|-------|-----|-----|-------------------------------|-------------------------------|----------------------------------|------------------------------------|---|--|
| A | High | F | 26 | 0 | 1.4 | 0 | 10 | 5.0 (4.6) | 5.1 |
| | Low | M | 28 | 10 | 10 | 10 | 4.3 | 4.1 (4.6) | 4.8 |
| B | High | F | 26 | 0 | 0 | 0 | 7.1 | 6.0 (5.7) | 5.4 |
| | Low | F | 25 | 8.6 | 7.1 | 5.7 | 4.3 | 2.7 (5.7) | 2 |
| C | High | M | 28 | 1.1 | 1.1 | 0 | 3.3 | 6.3 (4.4) | 4.7 |
| | Low | M | 29 | 10 | 5.6 | 4.4 | 1.1 | 3.1 (4.4) | 2.7 |
| D | High | M | 27 | 8.3 | 8.3 | 5 | 6.7 | 5.8 (4.4) | 4.8 |
| | Low | M | 24 | 10 | 6.7 | 7.5 | 5 | 3.8 (4.4) | 5.3 |

Note. Age = Years. Four tasks (No-Reward Tube and Mirror, Hard-Reward, Easy-Reward) = Converted rank relative to group size on a scale from 0 to 10. Lower scores correspond to a better rank; HE Proficiency Score = Mean proficiency score (out of 7) calculated from the sum of the three traits (7-point- Likert, 1 = least, 7 = most) across the three HEs; HE Dominance Score= Mean dominance score (out of 7) calculated from the sum of the three traits (7-point- Likert, 1 = least, 7 = most) across the three HEs; Text in bold indicates anomalies to expected rankings.

Main Experiment

Method

Subjects

One chimpanzee in group C died between the model selection phase and the open-diffusion phase of the study leaving a sample size of 53. Eight chimpanzees were used as models, two in each of groups A-D. The remaining 45 chimpanzees became the test subjects. During training, models voluntarily separated from group members. Training sessions (c 15mins) involved behaviour shaping and positive reinforcement. The open-diffusion phase of the study took place in the chimpanzees' large, enriched home enclosures (Primadomes, diameter 10m), and the chimpanzees had access to their inside dens at all times meaning that they chose whether or not to interact with the task.

Design

Chimpanzees identified as high past proficiency models (High PPM) and neutral-to-low past proficiency models (Low PPM) were individually trained to retrieve fruit from an out of reach basket using one of two distinct tools. Once the two models were proficient they demonstrated their tool use to their group in three 1hr sessions. Subsequently, two sets of apparatus and tools (two per apparatus) were made available to the whole group in four 2.5hr sessions. The remaining two groups served as no-model groups. These groups allow investigation of the influence of the trained models but, as chimpanzees were able to acquire social information from their group members' interactions with the task, they cannot be considered asocial learning control groups.

Apparatus

The study aimed to use a version of a two-solution extractive foraging task (Dawson & Foss, 1965; Whiten et al., 1996). Several two-action tasks were piloted with chimpanzees that did not take part in the main experiment. First, there was an adapted form of the Slide-Drawer-Box (SDB, Wood et al., 2013) with both manipulandi at the front. Chimpanzees were able to be trained on both methods, however, even in dyads it was very hard for the observer to see what the model was doing because the manipulandi were small and at the front of the box, blocked by the model's body. Reflecting on this, a task requiring larger apparatus was designed. Originally the two tools were 15cm tongs and a 15cm ladle. Chimpanzees found it hard to use these tools and the relatively short length of the tool meant that the food was only just out of reach and so the chimpanzees often attempted to use their hands to retrieve the food. The third revision involved the longer scoop and hook tools which required a combination of gross and fine motor skills.

There were two identical tasks. Each task (Figure 2) consisted of a cart placed by the bars, which were covered with square mesh with 5cm², outside of the chimpanzee's enclosure. On the cart was a hard plastic 7cm basket with a metal handle. The basket was situated 40cm away from the chimpanzees' enclosure and out of their reach. The edge of the cart was situated 10cm away from the bars so that the basket could not be dragged towards the window but had to be lifted off the cart for successful retrieval. Two tools per task, a scoop and a hook, were provided with the handle of the tool placed through the mesh. The scoop was a red 40cm steel rod with a steel garden hand spade (handle removed) melded on to it. The hook was a blue 50cm steel rod that at one end was shaped into a hook to make the final length 40cm. A 10cm piece of steel was welded 10cm from the handle end of the tool so that it could not be pulled into the enclosure (as the wire mesh fencing prevented this). Both tools could be used to obtain

the basket, either by scooping the bottom (scoop tool) or hooking the handle of the basket (hook tool). The basket was baited with a high value food reward: 2cm² chunks of watermelon, banana or mango. Each time a reward was obtained a new baited basket was placed onto the cart.

This task was again piloted and only two chimpanzees asocially learnt the task in a 60min period, both by dragging the basket. To prevent dragging, the baskets were placed on a cart which was 10cm away from the edge of the corral bars so that dragging would result in the basket falling between the gaps.



Figure 2: Baited task with either red scoop tool scooping (left) or blue hook tool hooking (right) to obtain the basket containing a high value food reward.

Procedure

Training Phase. Individually, the models were trained through shaping and positive reinforcement. Once the model had achieved 30 successful basket retrievals s/he was judged a reliable model and, assuming the opposing demonstrator was fully trained, the observation phase began. In all four groups the High PPM model took fewer training sessions to reach the criteria than the Low PPM although exact data for this was not recorded.

Observation Phase. Two carts were placed at each of two windows (1m x 1.5m with wire mesh) about 1.5m apart from each other. Each model was called to a window

and was handed the tool they had been trained to use. For example, in a group with the High PPM trained with the hook and the Low PPM trained with the scoop, at the start of the observation phase the High PPM approached window 1 and was handed a hook tool whilst a scoop tool was placed by the side of the apparatus in clear view of the other chimpanzees. After the High PPM's demonstration, the Low PPM was called to window 2 and was handed a second scoop tool and a second hook tool was placed by the side of the apparatus. The first hook and scoop tools remained in sight but unobtainable at window 1. Each model was handed their 'trained' tool regardless of the window they approached, thus a specific tool was not associated with a particular window by experimenter design. In this phase, which occupied 60mins on each of three consecutive week days, the model was allowed to operate the tools, but on the occasions that other chimpanzees acquired the tool, the experimenter did not bait the basket or, if the basket had already been baited, the experimenter withdrew the cart so that the basket became out of reach even with the tool. When one model was successful the experimenter did not re-bait this basket until the other model was successful and thus the demonstrations alternated between the two chimpanzees. If the model made contact with the basket but failed to hook/scoop it after 5s, the experimenter assisted by attaching the basket to the tool. If a model failed to approach the task or successfully retrieve a basket within 1min of the other model's last success the basket of the original model was re-baited. Through calling chimpanzee's names, and occasional assisted attachment of baskets, the experimenter attempted to obtain an equal number of demonstrations from both models, and for each observer to witness at least ten demonstrations in total

Open Diffusion Phase. The open diffusion was carried out over four sessions on separate days, each two-and-a-half hours long. Both carts were used and at each cart

the two tools were placed through the mesh. How the tools lay in relation to each other was counterbalanced within and between groups. Following a success the experimenter did not re-bait this cart until there was success at the other cart or 2mins had passed. This was to ensure an equal balance of the experimenter's time at each window and cart.

Coding and Inter-Rater Reliability

There were instances whereby a chimpanzee's interaction involved holding both tools or the use of the only tool available at the baited cart, i.e. another chimpanzee was holding the other tool. We therefore coded first interactions (henceforth 'absolute') and first interactions when both tools were available (henceforth 'free'). Each chimpanzee's performance was scored for, (a) which tool they first *touched* (absolute and free), (b) which tool they first *attempted* to retrieve the basket with, defined by the tool making contact with the basket (absolute and free), and (c) which tool they had their first *successful* retrieval of the food reward with (absolute and free). The first five attempts and successes of each chimpanzee were also recorded. Attempts and successes observed by conspecifics were recorded both prior to each individual's first success and between each success. The experimenter, LW, coded 100% of the sample from video tape. An independent observer coded 25% of the sample. There was disagreement on 0.67% of the trials double coded for tool touch and attempt. This was mainly due to a need for clarification over whether tool touches occurred simultaneously (within a few seconds and resulting in holding both) or sequentially (more than a few seconds in-between and not holding both). All first tool touches were coded again to ensure consistency. There were no disagreements for tool success.

Results

Demonstration Phase

There was no significant difference between the number of High PPM ($M = 8.67$, $SD = 9.07$) or Low PPM ($M = 7.70$, $SD = 6.49$) demonstrations seen (Wilcoxon $Z_2 = -.54$, $p = .59$, $d = .14$). The number of successful demonstrations across all groups for the High PPMs ($N = 182$) and the Low PPMs ($N = 182$) was equal. However the Low PPMs had a significantly higher proportion of failed attempts (Total $N = 276$, Failed $N = 94$, 34%) than the High PPMs (Total $N = 235$, Failed $N = 53$, 23%, Fisher's Exact Test; FET, $p < .001$). Thus, whilst the number of successes observed was equal the overall number of task interactions by the Low PPMs was greater than the High PPMs. Furthermore, the experimenter had to assist (model makes contact with basket but fails to attach after 5s so the experimenter attaches basket) the Low PPMs ($M = 40.0$, $SD = 11.2$) significantly more than the High PPMs ($M = 20.3$, $SD = 3.6$, FET $p < .001$).

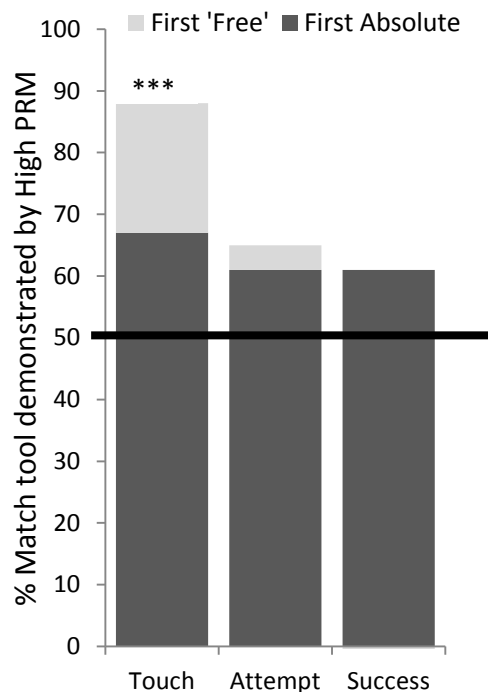
Success Rates for the Model versus No-model Groups

During the open diffusion phase, and across model and no-model groups, thirty-nine (87%) of the 45 untrained chimpanzees were successful at obtaining a reward, 24 of these did so in the first session. In the first session the model-groups had marginally more successful individuals (14/24; 58%) than the no-model groups (10/21; 48%) although this difference was not significant (FET, $p = .56$, $d = .10$). This pattern continued overall with 22/24 (92%) individuals of Model groups versus 17/21 (81%) individuals of no-model groups being successful (FET, $p = .40$, $d = .16$). Although the model group chimpanzees had fewer unsuccessful attempts before their first success ($M = 2.33$, $SD = 0.40$) than no-model group chimpanzees ($M = 3.05$, $SD = 0.48$) this difference was also not significant ($U = 203.5$, $p = .26$, $d = .99$). The rank scores of the

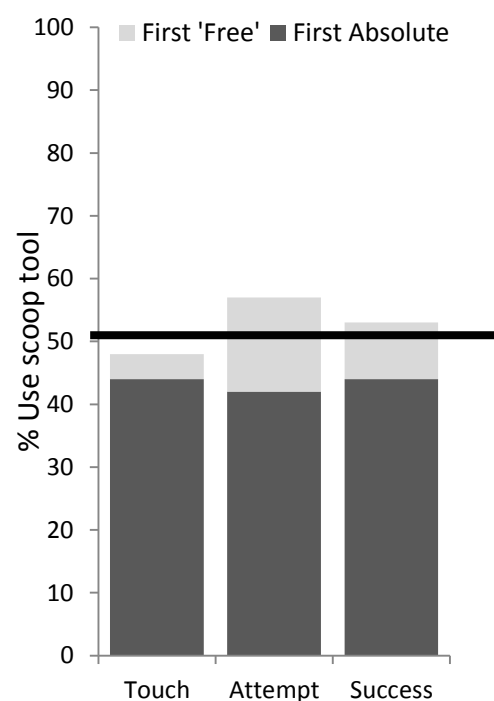
order in which each individual achieved their first success were standardised from a scale of 0 to 10 so that each chimp had a rank score relative to his/her group size. There was a significant positive correlation between order of success with a hook/scoop tool and performance with the four novel tasks combined ($r_s(43) = .55, p < .05$). Hence, those who were more proficient with the novel tasks were more likely to be successful with the tool task before those who were less proficient with the novel tasks.

First Interactions in Relation to Model Past-Proficiency

We predicted that naïve chimpanzees (no prior personal experience) who observed differing solutions from two models would initially copy the solution choice of the High PPM. We assessed this by looking at each chimpanzee's first tool touch, attempted tool use and successful basket retrieval.



3a Chimpanzees from model groups



3b Chimpanzees from no-model groups

Figure 3: Percentage of chimpanzees matching High PPM for model-groups (1a) or scoop for no-model group (1b). Note: 50% equals chance (as indicated by black line).

**** $p < .001$ significantly different from chance*

First touch. All 45 untrained chimpanzees made contact with at least one tool, 43 of these chimpanzees did so in the first session indicating that there was no neophobia towards the apparatus. Across all groups there were 11 instances whereby a chimpanzee's first touch involved holding both tools. There were also 12 occasions whereby a chimpanzee's first touch was with the only tool available at the baited cart. In the four model groups, for absolute first touch, 6 chimpanzees touched both tools, 12 matched the High PPM and 6 matched the Low PPM (Binomial for tool matching High PPM tool, $p = .24$, $d = .75$). For free first touch, 21 chimpanzees matched the High PPM and 3 matched the Low PPM (Binomial, $p < .001$, Figure 3). In the no-model groups there was no significant difference between tools for absolute first touch (hook $N = 9$, scoop $N = 7$, Binomial, $p = .80$, $d = .22$; both tools simultaneously $N = 5$) or free first touch (hook $N = 10$, scoop $N = 9$, Binomial, $p > .99$, $d = .20$; both tools simultaneously $N = 2$).

First Attempt. One chimpanzee made no attempt during the open-diffusion phase (he was not present in the fourth session due to injury, being the only chimpanzee to not be present for all four sessions). No chimpanzee in the model groups used both tools on their absolute first attempt, 14 of the 23 (61%) matched the High PPM and 9 (39%) matched the Low PPM (Binomial, $p = .40$, $d = .60$). On their free first attempt, 15 of the 23 (65%) matched the High PPM and 8 (35%) matched the Low PPM (Binomial, $p = .21$, $d = .86$). In the no-model-groups there was no significant difference between hook and scoop tool absolute first attempt (hook $N = 11$, scoop $N = 8$,

Binomial, $p = .65$, $d = .25$; both tools simultaneously $N = 2$) or free first attempt (hook $N = 9$, scoop $N = 12$, Binomial, $p = .66$, $d = .29$). The disparity between the extent of High PPM tool matching for first free touch and subsequent attempt was investigated (see Table 5).

Table 5: Chimpanzee behaviour in trials involving first free touch as categorised by High / Low PPM tool matching on first free touch and subsequent attempt.

| First free touch and attempt | ID | Behaviour in first free touch trial |
|---|----|-------------------------------------|
| Matches High PPM during free touch and attempt | Na | Attempts |
| | Lu | Attempts |
| | Ca | Attempts |
| | Da | Attempts |
| | St | Attempts |
| | Eh | Attempts |
| | Ke | Attempts |
| | Ta | Attempts |
| | En | Attempts |
| | Kp | Attempts |
| | Id | Displaced by conspecific |
| | Sa | Leaves 'voluntarily' |
| Matches High PPM during free touch but <u>not</u> attempt | Ly | Remains but does not manipulate |
| | Kz | Leaves 'voluntarily' |
| | Ma | Leaves 'voluntarily' |
| | Pa | Displaced by conspecific |
| | Kt | Expels tool |
| | To | Expels tool |
| | Hu | Expels tool |
| | Ka | Expels tool |
| Matches Low PPM during free touch and attempt | Bi | Attempts |
| | Kk | Attempts |
| Matches Low free PPM during free touch but <u>not</u> attempt | Ta | Remains but does not manipulate |
| No Attempt | Do | Leaves 'voluntarily' |

The majority (10/12) of chimpanzees whose first free touch and attempt matched the High PPM attempted the task during the same trial, not letting go of the High PPM tool they first touched. Of the other two chimpanzees, one was displaced and one left the window voluntarily before the end of the trial. For the eight chimpanzees who matched the High PPM on their first free touch but not on their first free attempt, half ($N = 4$) pushed the tool out of the mesh fencing. On these occasions the experimenter (LW) replaced the tool but after it was pushed out three times LW made no further effort to replace the tool. Two chimpanzees voluntarily left the window after their first touch, one remained and one was displaced. Of the three chimpanzees who matched the Low PPM in their first free touch, two also matched the Low PPM on their first free attempt, both within the same trial; one chimpanzee remained at the window for the remainder of the trial but never attempted a tool use.

First Success. No chimpanzee in the model groups used both tools on their absolute first success and one chimpanzee's first absolute success involved inverting the scoop and hooking with it. Thirteen of the remaining 21 (61%) matched the High PPM and 8 (39%) matched the Low PPM (Binomial, $p = .38$, $d = .56$). On their free first success, 12 of the 21 (57%) matched the High PPM and 9 (43%) matched the Low PPM (Binomial, $p = .66$, $d = .56$). In the no-model-groups there was no significant difference between hook and scoop tool absolute first success (hook $N = 9$, scoop $N = 7$, Binomial, $p = .80$, $d = .22$) or free first success (hook $N = 7$, scoop $N = 8$, Binomial, $p > .99$, $d = .09$; one chimpanzee hooked with the scoop).

Solution Choice over Trials

Each chimpanzee's absolute first five attempts and first five successes or their total number if less than five (see appendix for figures) were examined. Across the four

model-groups there was no difference between the number of successful tool uses that matched the High PPM ($M = 2.43$, $SD = 1.27$) and the Low PPM ($M = 2.26$, $SD = 1.36$, $t_{22} = 0.34$, $p = .74$, $d = .17$). The majority of chimpanzees showed a variety of tool use across their first five attempts. Of the 42 chimpanzees who had multiple attempts, significantly more chimpanzees used more than one tool solution ($N = 35$, 83%) than just one ($N = 7$, 17%, Binomial, $p < .001$, $d = .99$). There was no difference in this pattern of multiple tool use for basket retrieval attempts for chimpanzees in the model- versus the no-model-groups (FET, $p = .43$). A similar pattern was found when looking at the first five successes; of the chimpanzees who had more than one success, significantly more chimpanzees used more than one tool solution (23/31, 74%) than just one tool solution (8/31, 26%, Binomial, $p < .05$, $d = .99$) with no difference between chimpanzees in the model-groups versus the no-model-groups (FET, $p > .99$). Some chimpanzees from both the model-groups ($N = 3$) and the no-model-groups ($N = 5$) discovered a third solution whereby the scoop tool was turned upside down and used to hook the basket. On no occasion was the other tool unavailable on these occurrences. Six of these eight chimpanzees were female but this was not a significant sex difference (FET, $p = .12$).

Post-Hoc analysis

We tested a number of other factors that could potentially explain tool preference.

Tool efficiency. There did not seem to be a clear pattern of tool efficiency. Two model-groups (both with High PPM demonstrating Hook) and one no-model group showed no differences in the tool involved in failed attempts ($ps > .05$ FE). The other no-model group showed disproportionate failures with the scoop tool ($N = 422$, $p < .001$

FE) as did one model group with High PPM demonstrating scoop tool ($N = 380$, $p < .01$ FE). The other Model group with High PPM demonstrating scoop tool showed the opposite pattern with a disproportionate amount of failures coming from hook ($N = 471$, $p < .01$ FE).

Copying in proportion to that observed. Eleven chimpanzees saw more demonstrations from the High, than low, PPM; the first free touch of 9 matched the High PPM tool and 2 matched the Low PPM tool. Ten chimpanzees saw more demonstrations from the Low PPM; the first free touch of 9 matched the High PPM tool and two matched the Low PPM tool. Thus, there was no difference between which PPM was watched more and whether the first free tool touched matched the High PPM (FET, $p > .99$). Likewise, there was no significant correlation between the proportion of demonstrations observed involving a tool in the demonstration phase and the proportion of interactions involving that tool in the first five attempts ($r_s(21) = .22$, $p = .32$) or first five successes ($r_s(40) = .22$, $p = .19$).

Methods used and novel task proficiency. Comparisons were made between behaviour with the four novel tasks and the number of tool methods (scoop/hook/inverted scoop-hook) used in the open diffusion. As might be expected there was a significant negative correlation between the summed novel task rank (lower ranking representing more interaction with the tasks) and the number of methods used in the open diffusion ($r_s(43) = -.32$, $p < .05$); chimpanzees who were more proficient with the novel tasks used more tool methods, than chimpanzees who were less proficient. However, chimpanzees who used the method of hooking with the scoop tool ($N = 8$) did not have significantly better rank scores with the four novel tasks than those who did not ($U = 145.5$, $p = .85$).

Discussion

Model-based Biases

The model-based bias of past proficiency was investigated. Both models' performances had been observed by group members on four tasks presented recently in a similar context, alongside many years of interactions with tools and various forms of enrichment. Therefore, there was much opportunity for group members to establish a proficiency schema for these models. The High PPM was also more proficient in the actual task; learning the task more quickly in training and exhibiting a smaller proportion of failed attempts and experimenter assisted attempts in the demonstration phase. Chimpanzees were biased towards the tool seeded by the High PPM; with significantly more first tool touches corresponding to the tool used by the High PPM than the Low PPM. This bias was evidenced despite the Low PPMs actually providing an increased number of tool interactions, than High PPMs, during the demonstration phase. This is because whilst the number of successes observed across models was equal the Low PPMs required a greater number of unsuccessful attempts to achieve this.

It could be argued that another factor that co-varies with past proficiency is responsible for the bias towards the tool used by the High PPM. However, all model pairs were of a similar age, with no more than three years age difference, and in three of the four groups the models were the same sex. Although it was not possible to match individuals for dominance, there was no systematic pattern of dominance in relation to past proficiency. In two groups the High PPM was appreciably more dominant than the Low PPM, in one group the Low PPM was appreciably more dominant than the High PPM and in the fourth group the models were of approximately equivalent dominance.

Whilst Horner et al. (2010) found that chimpanzees preferentially copy the choices of older models that are of a higher rank and who have previously been more

proficient at similar tasks, this study is the first to explicitly investigate the influence of the past proficiency of known conspecifics whilst controlling for other factors. As has been found with children (Chapter V), the chimpanzees' bias towards behaviour demonstrated by the High PPM may indicate cognitive sophistication including reputation formation. Potentially, the chimpanzees track other conspecific's behaviour over time and commit relative performance to memory, enabling them to compare pairs of models; "A is more proficient than B", and use this to guide their behaviour. Alternatively, chimpanzees' learning from individuals may be guided by an intuition based upon prior experience rather than memory ('emotional book-keeping' as described for reciprocal exchanges in baboons, Frank & Silk, 2009) or an appraisal of the chimpanzee's performance with the test task. A bias towards learning from models with past proficiency in a certain domain is adaptive as their demonstrated solutions to a novel task are likely to be relatively proficient. When faced with divergent information chimpanzees were guided by the information imparted by the High PPM. Past proficiency may be one of many model-based biases used by chimpanzees. Chimpanzees' attention and learning may be influenced by model age (Biro et al., 2003; Horner et al., 2010), dominance (Bonnie et al., 2007; Kendal et al., in prep.), generosity (Subiaul et al., 2008) or a number of other physical, cognitive or interpersonal characteristics.

Social Learning Processes and Mechanisms

The general pattern of results indicated that chimpanzees from the model groups obtained success following fewer unsuccessful attempts than did chimpanzees in the no-model groups. However, this difference was not significant, contrasting with chimpanzee research demonstrating statistically significant increased success following

a social demonstration (Nagell et al., 1993; Tomasello et al., 1987). A lack of difference between the model and no-model chimpanzee groups may have been a result of a lack of statistical power as the sample sizes were small. Alternatively, it could imply that there was no social learning; that the models behaviour had no effect on the chimpanzees. There are several reasons why this is unlikely. First, the chimpanzees in the no-model group were not asocial learning controls. From the moment the first chimpanzee in each no-model group began interacting with the task the other chimpanzees were potentially acquiring social information. Second, we found that chimpanzees who observed differing solutions from two models initially touched the tool seeded by the high past proficiency model, indicating an influence of the models upon learning.

While the no-model group was not a true asocial control, many of the no-model group chimpanzees solved the task with little social information. That is, many of them solved the task before they observed another individual solving the task and did so after the same amount of attempts as chimpanzees in the model groups. Therefore, the tentative suggestion is that chimpanzees' reward retrieval methods were not copied but initial tool choice was socially influenced. Accordingly, chimpanzees may not have learned the form of the action from conspecifics as previous tool-use experience may have informed their first attempts and successes with either tool. These chimpanzees regularly receive enrichment including dipping bamboo sticks into pipes that contain a variety of attractive foodstuffs. Thus, these chimpanzees may be practised in handling a long tool and pushing it away from them to obtain food (a similar phenomenon was discussed by Hopper et al., 2007). Because the majority of chimpanzees initially picked up the High PPM's tool, the majority of chimpanzees also attempted this tool. However, for those whose first touch had been interrupted (e.g. they were displaced) or if they

made no attempt from their first touch (they walked away in that trial) their first attempt involved the Low PPM's tool.

Although chimpanzees are certainly capable of complex forms of social learning such as emulation and imitation (Nagell et al., 1993; Whiten, et al., 1996, 2005, 2007) I propose that the chimpanzees' learning was guided by model chimpanzees' past proficiency and simple social learning mechanisms, such as stimulus enhancement. This resulted in *biased stimulus enhancement*. This is stimulus enhancement because the model's behaviour increased the probability that the observer interacted with stimuli of the same physical type as those with which s/he interacted (Heyes, 1994) and it is biased as the resultant attraction to a tool did not occur irrespective of the identity of the model (Rendell et al. 2011). The biased aspect of the stimulus enhancement is supported by the fact that despite the overall number of task interactions being greater for the Low PPMs, individuals still touched the tool used by the High PPM first, indicating that the salience of one or other tool must have been influenced by something other than its frequency of use. Although such biased stimulus enhancement did not result in group homogeneity of behaviour in our study, such biased stimulus enhancement fits with the findings of Matthews et al. (2010) that traditions can result from an interaction of stimulus enhancement with individual learning.

It is possible that this biased stimulus enhancement may be underpinned by associative learning. Chimpanzees might associate the High PPM with more success (e.g. increased food reward). This association over time creates a model-based bias. This, however, is different from the argument put forward by Hoppitt & Laland (2008) that what appears to be stimulus enhancement may instead be manifestations of associative learning; the chimpanzees learn that a certain tool had a higher rate of success than another tool during the demonstration phase. In the current study, both

tools had an equal volume of success so it cannot be that there was a simple association of tool with reward but something more complex, corresponding to the identity of the model.

Solution Choice over Time

Boyd and Richerson (1985) suggest that learning one solution can inhibit further exploration of a problem, a phenomenon reported previously in chimpanzees (Hrubesch et al., 2009; Hopper et al., 2011; Marshall-Pescini & Whiten, 2008). However, chimpanzees in the current study attempted and were successful with both methods, even in their first five trials. Yamamoto et al. (2013) found chimpanzees replaced an asocially learned reward method with a subsequently socially demonstrated method. In their experiment, the newly adopted method was more efficient but in the current experiment it happened despite solutions being equivalent. Furthermore, the chimpanzees did not become canalised to the new tool but used both tools interchangeably. Our results reflect the flexible tool use demonstrated in the wild by chimpanzees (Sanz & Morgan, 2009).

There are several explanations as to why chimpanzees used both methods in the current study. First, the social demonstration of both methods simultaneously may promote multiple method adoption. In previous studies just one method has been asocially learned (Hrubesch et al., 2009) or socially demonstrated (Marshall-Pescini & Whiten, 2008) before the other method was demonstrated. This sequence of prior asocial/social learning, followed by success, followed by social demonstration, is quite different from two methods being demonstrated in very quick succession before initial observer interaction. This could be explored further by introducing alternate methods in different time frames, for example, at the same time, in quick succession or with a

considerable time delay. Second, the use of both methods in the current study could be due to the fact that the alternate method was actually demonstrated rather than just available (Hopper et al., 2007; 2011). Thus in this study, the information provided for both methods meant that there was minimal cost to individuals in adopting both tool solutions. Third, both methods may have been asocially learned with the number of methods used correlating with proficiency (including exploration) with the novel tasks. Even if both methods were asocially learned the chimpanzees still demonstrated flexibility in switching from one method to another.

Finally, biased stimulus enhancement, rather than higher fidelity mechanisms of social learning, may result in low fidelity to a particular method. Henrich & Gil-White (2001) argue that when animals use simpler mechanisms of social learning, rather than action imitation, proficiency model-based bias (or foraging rank-based biases) will not be maintained because even if chimpanzees can identify the model proficiency, they do not acquire the details of anyone's technique. This might explain why the tool choice was socially biased but the action (reaching for the reward) seemed to be asocially learned for both tools. Thus, the bias to the first tool touched or used was short lived. Similarly, research with wild meerkats (Thornton & Malapert, 2009) demonstrated that simple social learning mechanisms create behavioural traditions but not necessarily behavioural uniformity within groups.

Problem Solving Proficiency in Chimpanzees

This study enabled assessment of chimpanzee interactions with a range of novel tasks. There was evidence that the tasks used enabled an appropriate assessment of proficiency in chimpanzees; their behaviour was consistent across three of the four novel tasks as has been shown with very similar novel tasks given to groups of children

(Wood et al., in prep; Chapter V). Chimpanzees were assessed not only for successful food retrieval but also on their order (relative to group mates) of first approach and interaction with the tasks, as well as exploratory behaviours such as number of approaches and interactions and types of interactions. There was a significant positive correlation between behaviour on the four novel tasks and order of success, relative to group mates, on the test-task. Similarly, work with hyenas has demonstrated that individuals exhibiting a greater diversity of initial exploratory behaviours are more successful problem solvers suggesting that the ‘diversity of initial exploratory behaviours is an important, determinant of problem-solving success in non-human animals’ (Benson-Amram & Holekamp, 2012, p. 4087).

Additionally, the husbandry employees’ ratings of proficiency showed some degree of correlation with performance on the tasks suggesting that the tasks appropriately elicited the traits considered by the employees to assess proficiency. These traits were originally developed alongside a multitude of others which subsequently underwent factor analysis (Freeman Brosnan, Hopper, Lambeth, Schapiro, & Gosling, submitted). Freeman et al. found that these three traits also appeared to map onto a single construct and ratings were highly consistent across HEs. Finally, there was a significant positive correlation between order of success with the test task and combined rank for the four novel tasks; those who were more proficient with the novel tasks were more likely to be successful before those who were less proficient with the novel tasks. Taken together it seems evident that chimpanzees’ proficiency with novel tasks is stable over time and varying context and that this behaviour can be evaluated with behavioural assessments.

Future Directions

The test-task was easy enough to be learnt asocially in a relatively short time period. As these chimpanzees have much experience of tools both for enrichment and for research purposes, the challenge is to create tasks which may take significantly more time to be learned asocially than socially so that more complex social learning mechanisms and strategies can be investigated. Equally, the difficulty of the task may affect the strength of a particular model-based bias because the need for the most effective social information becomes more important. For example, Mesoudi & O'Brien (2008) and Mesoudi (2008) found that when finding the most successful outcome was relatively easy, individuals were less likely to source social information but when it was harder, individuals not only sourced social information but also selected the information from the individual with the highest proficiency. Thus, we might expect to find that as task difficulty increased, chimpanzees rely more on social information (as seen in Callitrichids; Kendal et al., 2009), particularly the social information provided by the High PPM rather than the Low PPM.

A strength of the current study was that the two tools were novel in their unique form and function. Whilst this enabled an investigation of the copying of tool choice and tool functions it also allowed for monopolisation of a single tool rather than the whole task. This meant that there were occasions when a chimpanzee could manipulate the task but only had access to one tool unlike other open-diffusion studies which have encountered whole task monopolisation (Lydia Hopper personal communication in regards to Hopper et al., 2007). Creating a paradigm where the actions of one chimpanzee (tool chosen) do not influence the options available to other group members would create neater categories of data and may have assisted in identifying model-based biases.

Another change in task design would be the addition of a third tool. This would allow for the investigation of whether the two model-demonstrated tools were preferentially selected over the no-model tool. This would help understanding of whether tool successes using the PPMs tool indicated a bias towards a particular model or a chance selection of one of the two tools. Additionally, it would further assist in our understanding of exploration and innovation; whilst the chimpanzees innovated a tool-use method (rotating the scoop and using the back to hook the basket) it is hard to discern whether they were copying the scoop tool, the hook method, both, or neither. An experiment using a task with three functionally different manipulandi has been undertaken with children and has demonstrated a relationship between model proficiency and the acquisition of third, undemonstrated methods (Wood et al., in prep; Chapter V).

Understanding biased learning might assist in the understanding of cultural transmission in wild chimpanzees. For example, it may assist in our understanding of why Biro et al. (2003, p.213) found that for instances of the cracking of novel nut species, chimpanzees in the wild were ‘highly specific in their selection of conspecifics as models for observation, attending to the nut-cracking activities of individuals in the same age group or older, but not younger than themselves’. However, in this same study Biro et al. found that juveniles were more likely than adults to explore and crack the novel nuts. Thus, there may not always be a correspondence between biases and the most adaptive behaviour. Additionally, chimpanzees in the wild might not have the opportunity to employ proficiency model-based biases because of social constraints; Lonsdorf and Bonnie (2010) argue that social tolerance of particular individuals may constrain behavioural demonstration on the part of the model and/or proximity of individuals to observe the behaviour. Thus, individuals may be more likely to learn

from those who tolerate their presence than those who have the best past proficiency. In working with BIZARRE (raised in Barren, Institutional, Zoo, And other Rare Rearing Environments; Leavens, Bard & Hopkins, 2010) captive chimpanzees one must acknowledge that behaviour demonstrated may reflect potential model-based transmission biases rather than the actual model-based strategies, if any, used in the wild. Accordingly, further research focussed on investigating such dynamics in the wild would shed further light on chimpanzees' natural social learning abilities.

Conclusions

The current study suggests that chimpanzees' tool-use behaviour is biased by the proficiency of a model. That proficiency pertains to the past and current behaviour of the model and implies chimpanzees employ short- or long-term knowledge regarding the 'reputation' of known conspecifics. Theoretical models of cultural evolution predict the evolution of flexible strategies influencing the circumstances under which individuals copy others and from whom they learn (Boyd & Richerson, 1985). This study suggests that a proficiency model-based bias is one such flexible strategy, which may allow populations to gain adaptive information more quickly than when learning is asocial or unbiased (in which individuals acquire variants in proportion to the frequency at which they are shown Rendell et al., 2011). Indeed, a copy successful bias found in humans (Mesoudi, 2008, 2011) has been used to test theoretical models of cultural evolution. Thus, the presence of model-based biases in chimpanzees indicates that chimpanzees could possess skills necessary for an adaptive socially learned behaviour to spread in a group and for culture to evolve.

Appendices

Details

Appendix 1. First five attempts from chimpanzees in the no- model (1a) and model (1b and 1c) groups. Bordered boxes indicate colour coded (blue= blue hook, red = red scoop) demonstrations observed before each trial. Non bordered boxes indicate colour coded attempts (lighter shades) or successful attempts (darker shades). Purple indicate hooking with scoop tool.

Appendix 2. First five attempts from chimpanzees in the no- model (2a) and no-model groups (2b and 2c)groups. Bordered boxes indicate colour coded (blue= blue hook, red = red scoop) demonstrations observed before each trial. Non bordered boxes indicate colour coded attempts (lighter shades) or successful attempts (darker shades). Purple indicate hooking with scoop tool.

Appendix 1a: First Five attempts in no-model group chimpanzees

| ID | Seen | Attempt 1 | Seen | Attempt 2 | Seen | Attempt 3 | Seen | Attempt 4 | Seen | Attempt 5 |
|----|-------------|-----------|---------|-----------|--------|-----------|--------|-----------|-------------|-----------|
| Ja | | | | | | | | | | |
| Xe | | | | | | | | | 1 | |
| Ju | | | | | | | | | | |
| Mi | | | 1 | | | | | | | |
| Be | | | | | 1 | | | | | |
| Ti | | | | | | | | | | |
| Je | | | | | | | 3 | | | |
| Mu | | | | | | | | | | |
| Ga | | | 1 2 | | | | | | 1 1 1 | |
| Le | | | 1 | | | | | | | |
| Pe | | | 1 | | | | | | | |
| Ax | | | 1 | | 1 | | | | | |
| Ho | 1 | | | | | | | | | |
| Mo | 1 | | | | | | 2 2 | | | |
| So | 1 | | | | | | | | | |
| Bo | 1 1 | | | | | | 1 | | | |
| Be | 1 1 1 | | | | | | 1 | | | |
| Bi | 1 2 | | | | 1 2 | | | | | |
| Ap | 1 1 1 | | 10 1 | | | | | | | |
| Ma | | | | | | | | | | |
| Ba | | | | | | | | | | |

Appendix 1b: First Five attempts in groups where High PPM used red scoop

| | Seen | | Attempt | Seen | | Attempt | Seen | | Attempt | Seen | | Attempt | Seen | | Attempt |
|----|------|---|---------|------|---|---------|------|---|---------|------|---|---------|------|---|---------|
| | M | O | 1 | M | O | 2 | M | O | 3 | M | O | 4 | M | O | 5 |
| LY | 41 | | | | | | | | | | | | | | |
| | 24 | | | | | | | | | | | | | | |
| DA | 24 | | | | | | | | | | | | | | |
| | 13 | | | 1 | | | 1 | | | | | | | | |
| CA | 10 | | | | | | | | | | | | | | |
| | 15 | | | | | | | | | | | | | | |
| SA | | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | |
| LU | 7 | | | | | | | | | | | | | | |
| | 7 | | | | | | 1 | 3 | | | | | | | |
| PA | 12 | | | | | | | | | | | | | | |
| | 3 | 3 | | | | | | | | | | | 1 | | |
| ST | | | | 5 | | | 1 | | | | | | | | |
| | 1 | | | | | | | | | | | | | | |
| KH | 8 | | | | | | | | | | | | | 1 | |
| | 1 | | | | | | | | | | | | | | |
| KA | 5 | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | |
| MA | 8 | | | 1 | | | | | | 1 | | | | | |
| | 6 | 1 | | | | | | | | | | | | | |
| KU | 2 | 1 | | | | | | | | | | | | | |
| | 10 | | | | | | | | | | | | | | |
| DO | 6 | | | | | | | | | | | | | | |
| | 10 | | | | | | | | | | | | | | |

Note. M = Model, O = Other conspecific

Appendix 1c: First Five attempts where High PPM used blue hook

| | Seen | | Attempt | Seen | | Attempt | Seen | | Attempt | Seen | | Attempt | Seen | | Attempt | Seen | | Attempt | Seen | | Attempt | Seen | | Attempt |
|----|------|---|---------|------|---|---------|------|---|---------|------|---|---------|------|---|---------|------|---|---------|------|---|---------|------|---|---------|
| | M | O | | M | O | | M | O | | M | O | | M | O | | M | O | | M | O | | M | O | |
| EH | 21 | | | | | | 1 | | | | | | | | | | | | | | | | | |
| | 25 | | | | | | | | | | | | | | | | | | | | | | | |
| KE | 15 | | | | | | | | | | | | | | | | | | | | | | | |
| | 8 | | | | | | | | | | | | | 1 | | | | | | | | | | |
| TO | 14 | 1 | | | | | | 1 | | | | | 2 | | | | | | | | | | | |
| | 8 | 1 | | | 1 | | | 2 | | | | | 2 | | | | | | | | | | | |
| | | | | | | | | | | | | | | 1 | | | | | | | | | | |
| HU | 2 | | | | | | | | | | | | | | | | | | | | | | | |
| | 14 | 1 | | | | | | | | | | | | | | | | | | | | | | |
| ID | 9 | | | 1 | | | | | | | | | 5 | 1 | | | | | | | | | | |
| | 7 | | | 1 | 6 | | | | | | | | | 1 | | | | | | | | | | |
| | | | | | | | | | | | | | | 2 | | | | | | | | | | |
| BI | 3 | | | | | | | | | | | | | | | | | | | | | | | |
| | 13 | | | | | | | | | | | | | | | | | | | | | | | |
| KU | 8 | | | | | | | | | | | | | | | | | | | | | | | |
| | 4 | 3 | | | | | | | | | | | | | | | | | | | | | | |
| NA | 8 | 2 | | | | | | | | | | | | | | | | | | | | | | |
| | 4 | | | | | | | | | | | | | | | | | | | | | | | |
| EN | 4 | | | | | | | | | | | | | | | | | | | | | | | |
| | 4 | | | | 1 | | | 1 | | | | | | | | | | | | | | | | |
| TA | 4 | | | | | | | | | | | | | | | | | | | | | | | |
| | 6 | 7 | | | | | | | | | | | | | | | | | | | | | | |
| KA | 4 | | | | | | | | | | | | | | | | | | | | | | | |
| | 3 | 1 | | | | | | | | | | | | | | | | | | | | | | |
| TH | 4 | | | | | | | | | | | | | 1 | | | | | | | | 7 | | |
| | 2 | | | | | | | | | | | | | | | | | | | | | 11 | | |

Note, M = Model, O = Other conspecific

Appendix 2a: First Five successes in no-model group chimpanzees

| ID | Seen | S1 | Seen | UAs | S2 | Seen | UAs | S3 | Seen | UAs | S4 | Seen | UAs | S5 |
|----|------|----|------|-----|----|------|-----|----|------|-----|----|------|-----|----|
| Ja | | | | | | | 2 | | | | | | | |
| | | | | | | | 2 | | | | | | | |
| Xe | | | 1 | | | 2 | 9 | | | | | | | |
| | 1 | | | | | | 6 | | | | | | | |
| Ju | | | | 1 | | | | | | | | | | |
| | | | | 1 | | | | | | | | | | |
| Mi | | NB | | | | | | | | | | | | |
| | 1 | | | | | | | | | 1 | | | | |
| Be | | | | | | | | | | | | | | |
| | | | 2 | | | | | | | | | | | |
| Ho | | | | 1 | | 1 | 5 | | | | | | | |
| | 1 | | | 1 | | 1 | 5 | | | | | | | |
| Je | | | 3 | | NB | | | | | | NB | | | |
| | | | | | | | | | | | | | | |
| Mu | | | | 1 | | | | | | | | | | |
| | | | | | | | | | | | | | | |
| Ga | 1 | | 2 | 1 | | | | | | | | | | |
| | 2 | | 3 | | | 2 | | | | | | | | |
| Le | 1 | | | 2 | | | 1 | | | | | | | |
| | 5 | | | 1 | | | 1 | | | | | | | |
| Be | 3 | | 1 | | | | 1 | | | | 1 | | | |
| | 2 | | | | | | | | | | 1 | | | |
| Bi | | | 1 | | | | | | | | | | | |
| | 1 | | | 1 | | | | | | | | | | |
| | 2 | | | | | | | | | | | | | |
| Ax | | | 2 | 1 | | 1 | 1 | | | | | | | |
| | 1 | | | 1 | | 1 | 3 | | | | | | | |
| Mo | | | 3 | 1 | | | | | | | | | | |
| | 1 | | 2 | | | | | | | | | | | |
| So | | | 3 | 10 | | | | | | | | | | |
| | | | 22 | 5 | | | | | | | | | | |
| Ap | 1 | | | 1 | | | | | | | | | | |
| | 1 | | 10 | | | | | | | | | | | |
| Bo | 1 | | 2 | 1 | | | | | | | | | | |
| | 1 | | | | | | | | | | | | | |
| Ba | 3 | | | | | | | | | | | | | |
| | 2 | | | | | | | | | | | | | |
| Ma | 2 | | | | | | | | | | | | | |
| | 11 | | | | | | | | | | | | | |
| Pe | 2 | | | | | | | | | | | | | |
| | 6 | | | | | | | | | | | | | |
| Ti | 4 | | | | | | | | | | | | | |
| | 20 | | | | | | | | | | | | | |

Note. NB= No Basket UAs = Unsuccessful attempts

Appendix 2b: First Five successes where High PPM used red scoop

| | Seen | | | | Seen | | | | Seen | | | | Seen | | | | Seen | | | |
|----|------|---|-----|----|------|---|-----|----|------|---|-----|----|------|---|-----|----|------|---|-----|----|
| | M | O | UAs | | M | O | UAs | | M | O | UAs | | M | O | UAs | | M | O | UAs | |
| Ly | 41 | | 1 | S1 | 1 | | | S2 | | | | S3 | | | | NB | | | | S5 |
| | 24 | | 2 | | | | | | | | | | | | | | | | | |
| Ca | 10 | 1 | | NB | | | 1 | | | | 3 | | | | 1 | NB | | | | |
| | 15 | | | | | | | | | | 1 | | | | | | | | | |
| Pa | 12 | 1 | | | | | 2 | | | | | | | | 1 | | | | | |
| | 3 | 4 | 1 | | | 1 | | | | | | | | | | | | | | |
| Da | 24 | | 3 | | 1 | 1 | | | | | | | 2 | 2 | 3 | | | | | |
| | 13 | 2 | 1 | | | | 1 | | | | | | | | 1 | | | | 1 | |
| Ka | 6 | | 3 | NB | | | | NB | | | 2 | | | | 1 | | | | 1 | |
| | | | 2 | | | | | | | | 2 | | | | 1 | | | | | |
| Ma | 8 | | | | | 1 | | | | | | | 1 | | | | | | | |
| | 6 | 1 | | | | | | | | | | | | | | | | 1 | 1 | |
| Kh | 8 | | 1 | | 2 | | 1 | | | | 1 | | | | | | | | 1 | |
| | 1 | | 2 | | | | 2 | | | | | | | 1 | | | | | | |
| Lu | 7 | 3 | 2 | | | | | | | | | | | | | | | | | |
| | 9 | 2 | | | | | | | | | | | | | | | | | | |
| | | | 1 | | | | | | | | | | | | | | | | | |
| Sa | | | 2 | | | 1 | 1 | | | | | | | | | | | | 1 | |
| | | | | | | | | | | | | | | | | | | | | |
| St | 6 | | 2 | | 3 | 2 | 1 | | | | | | | | | | | | | |
| | 1 | | 3 | | | 1 | 2 | | | | | | | | | | | | | |
| | | | | | | | 1 | | | | | | | | | | | | | |
| Do | 6 | 5 | | | | | | | | | | | | | | | | | | |
| | 10 | 1 | | | | | | | | | | | | | | | | | | |
| Ku | 2 | 1 | 5 | | | | | | | | | | | | | | | | | |
| | 10 | | | | | | | | | | | | | | | | | | | |

Note, M = Model, O = Other conspecific, NB = No Basket, UAs = Unsuccessful attempts

Appendix 2c: First Five successes where High PPM used blue hook

| | Seen | | | | Seen | | | | Seen | | | | Seen | | | | Seen | | | |
|----|------|---|-----|----|------|---|-----|----|------|---|-----|----|------|---|-----|----|------|---|-----|----|
| | M | O | UAs | S1 | M | O | UAs | S2 | M | O | UAs | S3 | M | O | UAs | S4 | M | O | UAs | S5 |
| Th | 4 | | | | | | | | | 8 | 1 | | | | | | 4 | 2 | | |
| | 2 | | | | | | | | | 2 | 2 | | | | | | 6 | 1 | | |
| Eh | 21 | | | | | | | | 1 | | | | | | | NB | | | | |
| | 25 | | | | | | | | | | | | | | | | | | | |
| Ka | 4 | | | | | | 1 | | | | | | | | | | | | | |
| | 3 | 1 | 1 | | | | | | | | | | | | | | | | | |
| Na | 8 | 2 | 1 | | | | | | | | | | | | | | | | | |
| | 4 | | 2 | | | | | | | | | | | | | | | | | |
| Bi | 3 | | 1 | | | 1 | 1 | | | | | | | 1 | | | | | | |
| | 13 | | | | | 1 | 1 | | | 1 | | | | | | | | 1 | | |
| Ku | 8 | | | NB | | 1 | | | | | | | | | | NB | | | | |
| | 4 | 3 | | | | 1 | | | | | | | | | | | | 1 | | |
| Hu | 2 | | | | | | | | | | | | | | | | | | | |
| | 14 | 1 | | | | | | | | | 1 | | | 1 | | | | | | |
| Id | 10 | | | | | | | | | 3 | 1 | | | | | | | | | |
| | 8 | 6 | 1 | | | | | | 1 | | 1 | | | | | | | | | |
| | | 1 | | | | | | | | | | | | | | | | | | |
| En | 4 | | | | | | | | | | | | | | | | | | | |
| | 4 | | | | | 3 | 1 | | | | | | | | | | | | | |
| Ta | 4 | | | | | | | | | | | | | | | | | | | |
| | 6 | 7 | 1 | | | | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | | | | | | |
| To | 14 | 1 | 2 | NB | | 1 | 3 | | | | | | | | | | | | | |
| | 15 | 3 | 1 | | | | 1 | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | | | | | | |
| Ke | 15 | 8 | 3 | | | | 1 | | | | | | | | | | | | | |
| | 10 | 2 | 2 | | | | | | | | | | | | | | | | | |
| | | 2 | | | | | | | | | | | | | | | | | | |

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Chapter 7

General Discussion

The aim of this thesis was to investigate social learning mechanisms and strategies relating to the characteristics of a model (the individual transmitting the information) and the prior experience of an observer (the individual acquiring the social information). Using experimental designs to mirror naturalistic settings children and chimpanzees were presented with artificial fruit tasks in a number of different contexts. This enabled an investigation of how social learning mechanisms and strategies were affected by the characteristics of a model, the prior experience of an observer, continued model demonstrations and repeated observer interactions with the task. The following sections discuss the findings regarding these factors, both in individual studies and across studies, in an attempt to synthesise the overall impact of this body of research upon our understanding of social learning mechanisms and strategies.

Model-based Biases

Model-based biases are biases towards information provided by a model with certain characteristics over another model with differing characteristics (Henrich & McElreath, 2003). The literature review in Chapter II outlined a significant number of model-based biases in children's copying behaviour arguing for the adaptive value of model-based biased learning. In Chapter III, two specific biases were investigated in children; one that represented a self-declared proficiency (model knowledge state) and one that represented a group-level indication (as generally adults are perceived as more proficient than children, Taylor, Cartwright and Bowden, 1991) of proficiency (model age). Relevant actions were imitated faithfully by children regardless of the model's

characteristics, suggesting that if models provide solutions children will be motivated to copy these solutions irrespective of model identity. Indeed, a similar pattern of behaviour was found in the study presented in Chapter V. When children, either with no experience or a personally learned successful experience, were shown two new solutions by peers, they copied either model in their first subsequent task interaction, irrespective of their relative characteristics (proficiency reputation). It seems intuitive that if a model provides a clearly viable solution their characteristics may become tangential. Instead, unbiased social learning (Boyd & Richerson, 1985), whereby the probability that a behaviour is acquired by an observer is proportional to the frequency of the demonstrations of that behaviour, occurs. Such an unbiased strategy would enable children to acquire behaviours common within their culture.

Yet there were notable occasions where the characteristics of the model did influence children's copying. Children who observed an adult versus a child (Chapter III) reproduced more causally irrelevant actions. The professed knowledge state of the model was less influential but there was a tendency towards higher imitation of irrelevant actions when demonstrated by a knowledgeable over an ignorant model. Additionally, the study presented in Chapter V demonstrated that fidelity to a personally discovered solution, and the likelihood of discovering a new solution, was influenced by whether solutions were presented by models with differing proficiency characteristics. When the higher, rather than lower, past-proficiency model matched the child's original solution the child was more likely to keep using this solution. Having a higher-proficiency model match one's behaviour might increase confidence in one's solution. This resonates with the report that adults are increasingly unlikely to adopt a different method with increasing confidence in their own method (Morgan, Rendell, Ehn, Hoppitt & Laland, 2012). Conversely, when the lower past-proficiency model matched the

child's original solution and the higher past-proficiency model offered an alternative, children were more likely to discover previously untried and unseen solutions. Such motivation to explore artefacts, after proficient models demonstrate alternatives, could lead to improved artefact knowledge. This knowledge and exploration could result in improvement being made to tasks over time. Hence it could be a contributing factor in artefact 'ratcheting' resulting in cumulative culture (Tennie, Call & Tomasello, 2009).

These empirical studies provide evidence that young children do not source information indiscriminately but rather use model-based biases to guide their learning. This supports two arguments presented in the review (Chapter II): first, model-based biases are adaptive as they enable children to source behaviour from the best model (Henrich & McElreath, 2003). Children showed higher fidelity copying of models who either were more proficient, or belonged to an age group that children generally regard as more proficient (Taylor, Cartwright & Bowden, 1991). This adaptiveness has been argued more generally for biases in social learning. For example, Laland (2004) and Boyd and Richerson (1985) predict the evolution of flexible strategies (or transmission biases) enabling avoidance of unreliable information, and model characteristics seem a likely candidate as they influence the circumstances under which individuals copy others and from whom they learn.

Second, for certain model characteristics to bias learning children need cognitive skills such as behaviour monitoring and mental state understanding. Children demonstrated biases towards past-proficiency and knowledge-state. While there is evidence for mental state understanding in chimpanzees (Call & Tomasello, 2008), the combination of mental state understanding and the language ability necessary to understand a model's declared knowledge state in Chapter III is a skill thought not to be possessed by other animals. Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello

(2007) argue that these species-specific socio-cognitive skills give humans a supreme ability for living in and exchanging knowledge in cultural groups. Surprisingly, children favoured the use of a ‘copy adults’ bias over a ‘copy task-knowledgeable individual’ bias (Chapter III), even though the latter could potentially have provided more reliable information. A similar pattern of behaviour has been found in adults whereby model prestige information and model success-related information were used to the same degree even though the former was less useful in achieving the optimum goal than the latter in this experiment (Atkisson, O’Brien & Mesoudi, 2012). While some model characteristics (e.g. age) are more physical and cognitively salient, others, such as professed knowledge state, are more subtle and require sophisticated socio-cognitive skills. An understanding of age develops earlier than an understanding of knowledge (Edwards, 1984; Wellman, Cross & Watson, 2001) so even though five-year-olds pass theory-of-mind tasks there could be a delay before model knowledge-state becomes a stronger bias than model age. This delay may be caused by a discrepancy between a salient age characteristic and a cognitively demanding knowledge-state, which should decrease with development until knowledge-state becomes the favoured bias as its informativeness outweighs the costs of its application.

While there have been many social learning experiments involving chimpanzees (see Whiten, McGuigan, Marshall-Pescini & Hopper, 2009) there is little empirical research investigating model-based biases in chimpanzees. In Chapter II, comparative perspectives were discussed demonstrating that a wide range of animals, from fish to chimpanzees, demonstrate model-based biases pertaining to model’s intentions (Buttelmann, Carpenter, Call, & Tomasello, 2007), proficiency (Duffy, Pike, & Laland, 2009), observer-similarity (Swaney, Kendal, Capon, Brown, & Laland, 2001), status (Bonnie, Horner, Whiten, & de Waal, 2007) and a combination of age, dominance and

previous proficiency (Horner, Proctor, Bonnie, Whiten, & de Waal, 2010). Furthermore, Kendal et al. (in prep) isolated five separate transmission biases operating simultaneously in chimpanzees including model-based attention biases relating to higher, versus lower, rank and proficiency.

Chapter VI introduced a novel tool-use paradigm to investigate model-based biases in chimpanzees. The first tool touched by chimpanzees was significantly more likely to match the tool demonstrated by a model with a higher proficiency-reputation than a lower proficiency-reputation. Chimpanzees, thus, seem able to track other conspecifics' behaviour over time and use this to guide their behaviour. Horner et al. (2010) labelled an older, more dominant chimpanzee with more past-proficiency (as rated by husbandry staff) as more 'prestigious' than a younger, less dominant and less previously proficient chimpanzee. As much as possible, we controlled for age and dominance and still found a bias for prior proficiency. To the extent that past-proficiency may be involved in a prestige bias, it is relevant to note that Henrich & Gil-White (2001) argue that dominance is distinct from prestige and relates to the skills and knowledge of a model within a given environment. Henrich & Gil-White (2001) also argue that many group living animals have the ability to rank the foraging ability of conspecifics. This ability allows individuals to target their attention preferentially toward models with high-quality skills. However, they also argue that marrying the ability to appraise models and learning differentially based on these appraisals will not occur in animals as they do not to imitate modelled actions. Thus, according to their argument, even if chimpanzees can identify model proficiency, they do not acquire the details of a specific model's technique. This might explain why the chimpanzee tool choice was biased towards the model with the higher past-proficiency tool but specific methods for retrieval were not biased. However, we know that chimpanzees are capable

of more complex forms of social learning (Nagell, Olguin, & Tomasello, 1993; Whiten, Custance, Gomez, Teixidor & Bard, 1996; Whiten, Horner & de Waal, 2005; Whiten et al., 2007) and so there is potential for model prestige, if defined as use of past-proficiency, to influence chimpanzees' learning.

There were significant differences in the way in which model characteristics were seen to bias learning between children and chimpanzees in this thesis. Model-based biases demonstrated by the children were apparent when looking at the reproduction of modelled irrelevant actions and task exploration beyond the two modelled methods. Neither of these behaviours were directly addressed in the chimpanzee study because the model chimpanzees were not trained to perform irrelevant actions and there were only two tools available, both of which were socially demonstrated.

When examining children's and chimpanzee's behaviour relating to the past-proficiency of known conspecifics, children with no prior interaction and then social information (in Chapter V) are the most comparable group to the chimpanzees. These children did not show a model based-bias towards either model; the manipuland they touched first was the manipuland they attempted and were successful with first and it was equally likely to be the manipuland demonstrated by either model. They then used either method with equal frequency. This stands in contrast to chimpanzees, with no prior personal interaction and social information, who showed a bias towards the tool seeded by the higher past-proficiency model. While interesting, it is difficult to know what might have caused this difference in behaviour because the studies differed in a number of important ways: (1) the chimpanzees knew their group mates for between 1.5 to 36 years whereas the children had known each other for between nine months to five years. (2) The chimpanzees had three hours of demonstrations, whereas the children had

two brief simultaneous video clips. (3) The task designs were very different in that the children used the SDLB three-action task box whilst the chimpanzees used two tools to access out-of-reach food.

The aim of this body of work was not to directly compare the behaviour of chimpanzees with that of children but to see how each group's behaviour might inform our understanding of their learning strategies. This, in turn, aids our understanding of cultural evolution. Humans are not unique in their ability to socially learn or to have social learning strategies, or indeed even to be biased towards particular model-based characteristics. However, this does not mean that humans and chimpanzees have identical model-based biases or that these biases affect these two species' learning in the same way. Two potential species differences in model-based biases are proposed. First, socio-cognitive skills, thought to be uniquely human (Herrmann et al, 2007), enable humans to better ascertain who is the best model in certain contexts. For example, as discussed earlier, the model-based bias of knowledge-state requires mental state understanding and sophisticated language ability and these are unique to humans. However, such a skill allows humans, from a certain age, to ascertain who the best model is.

Second, model characteristics bias different mechanisms differentially so that biased stimulus enhancement may only affect what is initially touched (Chapter VI) whereas biased imitation of causally irrelevant actions may affect the way in which the whole task is interacted with (Chapters III and V). The implication is not that chimpanzees are incapable of model-biased imitation. However, given the established literature indicating that children consistently show higher levels of imitation than chimpanzees (Call, Carpenter & Tomasello, 2005; Nagell et al., 1993; Whiten et al., 1996), it is reasonable to suggest that children will be more influenced by model-based

biases than chimpanzees who, while able to imitate, often use lower fidelity social learning mechanisms.

Multiple Interactions and Exploration

The study in Chapter III demonstrated that after an initial model demonstration and observer interaction with a task, children's behaviour can change following a second, identical demonstration and interaction. Here, children who observed knowledgeable models, reproduced more irrelevant actions at their second task attempt than at their first, while children observing ignorant models showed no change across their attempts. This propensity to change one's task behaviour was more thoroughly explored in Chapter IV. Here, some children were presented with a reward retrieval task and given a social demonstration of a solution followed by further solution matching or solution alternate information. Rather than remaining canalised to their initial solution, children attempted the alternative solution, incorporating both solutions into their repertoire. A similar finding was found in the study presented in Chapter V whereby children incorporated both solutions they saw the two models perform.

The relationship between asocial information and subsequent social information was also investigated in the studies presented in Chapter IV and V. Children with no (asocial) prior task interaction copied subsequent social information faithfully but failed to discover solutions beyond those demonstrated. However, children who interacted with the novel task before observing a social demonstration were significantly more likely to find more than one solution. Children with a prior personal interaction ultimately incorporated personal and social solutions into their repertoire, and discovered additional combination-solutions. This result appears to contrast with the large body of evidence from animals (reviewed by Kendal, Coolen, van Bergen &

Laland, 2005) indicating that if personal information is sufficient social information will be ignored. Moreover, the influence of prior personal exploration was attenuated by its outcome; children whose prior personal exploration had initially been unsuccessful were less likely to use a solution they had not seen subsequently demonstrated than children who had been successful in their initial personal exploration. It would appear that personally acquired information encourages exploration, beyond the use of social information, as long as this personally acquired information inspired confidence in the child (resulted in success).

Taken together, the role of prior experience seems extremely important in the acquisition of subsequent socially demonstrated behaviour. Social information provided to naïve or unsuccessful children, can result in the canalisation of behaviour, potentially highlighting a cost of social learning. Cost in this context refers to the inability to find additional solutions which, as discussed earlier, provides generalisable knowledge and increases one's overall knowledge of the task. However, even when children demonstrated initial canalisation, continued interaction encouraged a minority of children to discover additional solutions so the cost may be short lived. Children's ability to acquire multiple strategies to a problem has implications for our understanding of human cultural evolution; learning multiple strategies provides generalisable knowledge which is beneficial in a changing environment where there is potential for one solution to become obsolete (Boyd & Richerson, 1985). Humans have managed to inhabit the majority of the earth's enormously varied land habitats. The ability to generalise learning in different contexts enables humans to 'choose, regulate, construct and destroy important components of their environments' (Laland, Odling-Smee & Feldman, 2001, p.22). This 'niche construction' has enabled culture to evolve. Additionally, learning multiple strategies increases one's overall knowledge of the task

and the more knowledge one has of a task the more potential there is for modifications ('ratchet effect') which, over time, could lead to cumulative culture (Tennie, et al., 2009).

The chimpanzees (Chapter VI) also used both solutions over several interactions with the novel tool use task. Unlike children and previous work with chimpanzees (Hrubesch, Preuschoft, & van Schaik, 2009; Hopper, Schapiro, Lambeth and Brosnan, 2011) very few chimpanzees, from either the model or no-model groups, showed canalisation to one tool-use method. There are several explanations for this. First, perhaps chimpanzees learned both methods asocially and asocial learning corresponded with the individual levels of exploratory behaviour. Support for this comes from the significant correlation between chimpanzee performance with the novel tasks and the number of tool-use methods used in the open diffusion. Thus, chimpanzees that were more proficient with the novel tasks (including demonstrating greater exploration) used more methods on the test-task, than chimpanzees that were less proficient. Second, considering that the majority of chimpanzees, even those from the no-model groups would have seen some social information, the social influence cannot be dismissed. Thus, the chimpanzees, like the children, could have been motivated to acquire methods they witnessed. Being shown both methods, rather than just one, might explain why the results contrast with studies that have not demonstrated an alternative to chimpanzees (Hopper, Spiteri, Lambeth, Schapiro, Horner and Whiten, 2007) or children (Hopper, Flynn, Wood & Whiten, 2010). Thus in this study, the information provided for both methods meant that there was minimal cost to individuals in adopting both tool solutions. Third, chimpanzees in the current study learnt successful retrieval in a relatively short amount of time and often with very little or no social information. This contrasted with previous studies (Hopper et al. 2010; Whiten, et al., 2007) where

learning seemed to require a more sophisticated learning mechanism. As discussed earlier, simpler learning mechanisms may result in less fidelity to a particular method (Henrich & Gil-White, 2001).

Learning Mechanisms

Social learning mechanisms (Whiten & Ham, 1992) range from stimulus enhancement to complete action imitation. Whiten, Horner, Litchfield, & Marshall-Pescini (2004, p.36) argue that chimpanzees might employ, ‘a portfolio of alternative social-learning processes in flexibly adaptive ways, in conjunction with nonsocial learning’. In Chapter VI the chimpanzees appeared to be using biased stimulus enhancement in order to ‘choose’ which one of two tools to initially interact with. As some chimpanzees learned to use the tools with little or no social information the task used in Chapter VI seemed relatively easy. When tasks have been harder (as evidenced by chimpanzees with no social information failing to succeed at the task) chimpanzees use different mechanisms (e.g. goal emulation or action imitation; Tomasello Davis-Dasilva, Camak, & Bard, 1987; Whiten, et al., 1996, 2005, 2007). Thus, there is flexibility in the social learning mechanisms chimpanzees use dependent on context relating to task difficulty. Mesoudi & O’Brien (2008) and Mesoudi (2008) found that when the most successful outcome is relatively easily obtained, individuals are less likely to source social information but, when it is harder, individuals not only source social information but also select the information from the individual with the highest proficiency. Thus, we might expect that as task difficulty increases chimpanzees rely more on social information and employ higher fidelity copying, potentially extending their model-based bias to actual methods/actions rather than just initial attraction to one method over another (as in Chapter VI).

Conversely, children have been labelled ‘blind imitators’ (Want & Harris, 2002) who ‘replicate both the form and the goal of an observed behaviour but fail to understand the affordances of the objects involved in that behaviour or the link between the actions and the goal they subserve’ (p.3). Indeed, various studies of social learning in dyads whereby a naïve (no prior task experience) child observes an unfamiliar adult and shows high fidelity imitation (Flynn & Whiten, 2008b; Hopper et al., 2010; Horner & Whiten, 2005; Lyons, Young, & Keil, 2007). This high fidelity copying can lead to the reproduction of causally irrelevant actions (Horner & Whiten, 2005; Lyons et al., 2007). However, the body of research presented in this thesis demonstrates that children are not ‘blind imitators’ and that the ecologically realistic experimental designs used here demonstrate an immense amount of flexibility in children’s learning mechanisms, especially when coupled with social learning strategies or transmission biases. This is discussed below.

First, the study in Chapter III (age and knowledge state model characteristics) demonstrated that the identity of the model could affect social learning mechanisms within a single task; children observing adults imitated all modelled actions, including causally irrelevant actions, whereas children observing children copied the relevant door action but omitted the demonstrated irrelevant actions. If individuals parse out causally irrelevant actions but retain the relevant ones this learning mechanism may be best described as *goal imitation* rather than goal emulation or action imitation. If the term goal imitation is accepted, it can be said that the identity of the model affects which learning mechanism is used; action imitation when the model is adult, goal imitation when the model is a child. Similarly, the study in Chapter IV (involving multiple interactions and demonstrations) indicated an interaction between personally acquired information and social learning mechanisms; children, who acquired a solution through

personally acquired information, copied a subsequently demonstrated solution.

However, these children omitted the irrelevant actions to a greater extent than children without prior personal (but with prior social) information. It was not that children did not copy the model. Instead, they used goal imitation rather than action imitation.

Unfortunately, an attempt to replicate the child study presented in Chapter IV with chimpanzees proved unsuccessful because the chimpanzees did not attend to model chimpanzees presented via video recordings or live, possibly due to separation from the group or because the task was too small to be observed properly.

Third, when each child observed two models demonstrating causally relevant and irrelevant actions (Chapter V), children showed the least reproduction of causally irrelevant actions by children. This may have been a result of the demonstration mode; demonstrations were shown simultaneously and via video. However, the children were able to copy peer-modelled causally relevant solutions showing goal imitation without irrelevant action reproduction. The only condition that showed a pattern towards irrelevant action reproduction was for those children who were unsuccessful during their original attempt, as was found in the study presented in Chapter IV. It seems more likely that confidence in one's own performance followed by a demonstration from two known peers resulted in goal imitation rather than action imitation.

In summary, it appears that the combination of successful prior personal interactions, and known-peer-model demonstrations (as opposed to demonstrations from unfamiliar adults), diminishes 'blind' action imitation and results in goal imitation. This combination of factors more accurately reflects a child's normal learning environment. For example, in a nursery school a child might interact with an artefact before observing a degraded (i.e. noisy environment, other children playing with other toys, models not in plain sight) demonstration of known peers interacting with the toy. In these

circumstances children are far from blind imitators; they are sophisticated social learners who also employ a portfolio of alternative learning mechanisms in flexibly adaptive ways.

Evaluation of Experimental Methods

Participants

Four- to six-year-old children were the selected human sample because a large body of work investigating social learning strategies and mechanisms has been conducted with children of this age range (e.g. Flynn & Whiten 2008a, 2008b; Horner & Whiten, 2005; Koenig & Harris, 2005; McGuigan, Makinson, & Whiten, 2011; McGuigan Whiten, Flynn & Horner, 2007). Furthermore, at this age children are beginning to understand the knowledge states of others (Wellman et al., 2001) and the relationship between age and knowledge (Edwards, 1984). In choosing such a narrow age range it has to be accepted that only a snapshot of development can be obtained (See *Future Directions* below).

Chimpanzees were chosen because of their biological similarities and shared evolutionary history with humans. Furthermore, their behaviour in the wild reflects cultural behaviour and previous work with captive chimpanzees exemplifies their ability to socially learn complex tool use. In working with captive chimpanzees one must acknowledge that they are BIZARRE (raised in Barren, Institutional, Zoo, And other Rare Rearing Environments; Leavens, Bard & Hopkins, 2010). Leavens et al. argue ‘that there is no rational justification for overgeneralizing from BIZARRE chimpanzees to the entire chimpanzee species... no single environmental context can elicit the full range of chimpanzees’ cognitive capacities’ (p. 101). Thus, chimpanzees’ rearing

environments need to be carefully considered when interpreting the results of studies and extrapolating regarding behaviour demonstrated in the wild.

Work presented in this thesis demonstrated biased stimulus enhancement so one cannot know whether the model based bias exhibited in the captive chimpanzees would be stronger or weaker (or present at all) in wild chimpanzees. While the chimpanzees in the current study were captive, every attempt was made to use an experimental design that reflects learning conditions in the wild. First, the chimpanzees were permanently socially housed with individuals they had known for many years and, for a significant proportion, with whom they were related. Second, throughout the interaction with the novel tasks and the test-tool use task chimpanzees remained in their groups rather than being isolated and exposed to only one model. Third, the models were known conspecifics and demonstrations of tool use took place over an extended time frame and were live rather than video presentations.

Tasks

All experiments in the thesis utilised a variation of multi-action artefact tasks first implemented by Dawson & Foss (1965) and Whiten et al. (1996). Such tasks allow for a distinction between a number of learning mechanisms including asocial learning, goal emulation, action imitation and the reproduction of casually irrelevant actions ('overimitation'). Building upon this design, the children's tasks were designed to allow for further social learning investigation; first, the Slide-Drawer-Box was designed with the intention that it could be solved asocially by about two-thirds of children (and socially learnt by all children). This allowed for an investigation of the interaction between prior personal experience and subsequent social information. Second, the Slide-Drawer-Lever-Box, with its third manipulandi, enabled an investigation of the

relation between prior personal information and subsequent social information from differing models. Additionally, both tasks allowed for the measurement of additional exploration beyond already asocially learnt and socially demonstrated solutions. These tasks were effective in the experiments and could be used in future research.

For the chimpanzees two novel tools were created. These tools enabled individuals to access food that was out of reach. Training high-past-proficiency models to use either tool was relatively easy compared to low-past-proficiency models. Also, both tools could be asocially learnt in a relatively short amount of time which made it hard to distinguish whether tool use represented asocial or (biased or unbiased) social learning. The inclusion of a third tool may have assisted with this distinction. Here, models could be trained on the two tools and a third tool could be available. Then comparisons between the use of the non-demonstrated tool could be made with the two demonstrated tools to distinguish between asocial and social learning. Creating tasks for captive chimpanzees is always challenging; they need to be novel which is not easy in an enriched facility, they need to be within the chimpanzees' motor skill range and they need to be incredibly sturdy. To create such tasks, it seems important that different research labs communicate with each other regarding the successes and limitations of each of their designs.

Multi-action artificial-fruits are excellent artefacts for investigating social learning but have their limitations. They are made of man-made materials with, at times, man-made components (such as doors, bolts and baskets). These man-made components may be commonplace in a child's environment but not in a chimpanzees'. Thus, using the same tasks across species may exaggerate human social learning ability in comparison to other species. Second, artefact and tool-use tasks limit generalisations pertaining to social learning of behaviours beyond artefacts and tool-use. Much human

and non-human behaviour (e.g. play in children; grooming and hand-clasping in chimpanzees, Whiten et al., 1999) is not geared towards interacting with their natural or man-made environment but geared towards other goals including appropriate interpersonal interactions. Accordingly, much of this social behaviour may also be socially learnt. Understanding the mechanisms (e.g. contagion in agonistic encounters in captive chimpanzees; Videan, Fritz, Schwandt & Howell, 2005) and strategies underpinning ‘social’ social learning may be a far greater challenge, particularly in non-human animals.

Experimental Design

As outlined by Whiten & Mesoudi (2008; Mesoudi & Whiten, 2008) there are a variety of useful designs when investigating social learning, each with advantages and limitations. This body of work used variations on linear dyadic interactions for the children and open-diffusion interactions for the chimpanzees. Open-diffusion represents an ecologically valid design whereby whole population groups may be introduced to novel behaviours and behavioural spread can be monitored. A variant (two models rather than the traditional one) of this open-diffusion method was chosen for the chimpanzees for this reason but also because practically it is more optimal than studies involving a large degree of separation of pairs or trios of individuals. The challenge of open-diffusion is that the analysis of behaviour is much messier (Whiten & Flynn, 2010; Whiten & Mesoudi, 2008) as when initial observers interact with the task they are now also models. It is intended to undertake further complex analysis with the chimpanzee data to gain a deeper understanding of these effects, including Bayesian methods (e.g. Kendal et al. in prep.) and the use of other packages specifically written for such situations (e.g. Option Bias Analysis; Kendal, Kendal, Hoppitt, & Laland,

2009; Network Based Diffusion Analysis; Hoppitt & Laland, 2011). Group diffusion also entails issues of task monopolisation and intergroup conflict which may mask individuals' social learning abilities. However, such issues are off-set by the likely reduced stress (and likely preserved cognitive abilities) experienced by individuals when not isolated.

An open-diffusion design was not selected for children. This was because the research questions required maximum control over the child's previous personal experience, the subsequent social experience and who demonstrated what and when. Therefore a dyadic design, in which a single child participant watched another individual demonstrating, was adapted and used. This design also enabled direct comparison with previous research using similar dyadic designs (e.g. Horner & Whiten, 2005). The children watched different models ranging from unfamiliar adults to familiar peers to puppets. Children seemed comfortable when separated from their group (class) and dyadic learning occurs in children's natural environment (school) so this design remains relatively ecologically valid for children.

Future Directions

Tracking the Developmental Change of Model-based Biases

Investigating five-year-old children's model-based biases has been fruitful. Moving forward, a longitudinal or 'microgenetic approach' (Flynn, Pine & Lewis, 2007), whereby the development of individual children is tracked, would greatly assist our understanding of how socio-cognitive skills may assist with the development of biases relating to different model characteristics. For example, one could evaluate the microgenetic development of theory-of-mind skills (Flynn, 2007) alongside a

knowledge-state transmission bias. Additionally, the dynamics between biases involving multiple model characteristics could be investigated in a similar way. Such an investigation may assist in our understanding of what skills are necessary for biases to develop and thus why we might, as a species, show unique breadth in our culture.

Investigating Model-based Biases in Non-goal Directed Tasks

Our understanding of social learning mechanisms and strategies is limited by the use of goal-directed tasks. An interesting future direction, particularly in children, is to look at how model-based biases affect non goal-directed behaviour. Work in this field has begun; preferences (e.g. for food, clothes, toys and games) shown by children indicate biases towards familiar versus unfamiliar models (Shutts, Kinzler, McKee, & Spelke, 2009), same-sex (over different-sex) peers and, unlike novel artefact behaviour, children over adults (Shutts, Banji, & Spelke, 2010). Further, imitation of parents is more likely to consist of goal directed motor skills (e.g. tool-use) whereas non-goal directed affective behaviours are imitated from siblings and peers (Kuczynski, Zahn-Waxler, Radke-Yarrow, 1987). Thus, there may be some contexts whereby model-based biases are consistent for goal and non-goal directed behaviour and others where the biases may be less strong or even reversed.

Interactions of Biases

As outlined at the start of this chapter, the combinations of characteristic model traits that might bias learning are almost infinite. The challenge now is not only to investigate biases towards certain model characteristics but the relationship between different model-based biases. Chapter III demonstrated that biases towards one model characteristic (i.e. age) might overshadow a different model characteristic (i.e.

knowledge state). This result not only informs us about the specific model-based biases but it tells us something about the potential hierarchy of implementation of transmission biases. Additionally the dynamic between two biases (age and knowledge state) was only investigated at one point in children's development and the dynamic might alter during ontogeny. Research with adults demonstrated that a hierarchical strategy prioritised a success bias over a conformity bias although the latter was used when the payoff of behavioural options was indistinguishable (McElreath, Bell, Efferson, Lubell, Richerson, & Waring, 2008) and prestige information and success-related information were used to the same degree (Atkisson et al., 2012). Future research may ambitiously attempt to understand the dynamics between different model-based biases, context and cognitive development. Understanding this relationship could assist in our broader understanding of culture. For example Atkisson et al. (2012) argue that the equal use of success and prestige characteristics of models indicates that their participants are used to using prestige cues in their everyday lives as a short-cut to acquiring useful information.

Continuing to Develop Ecologically Valid Designs

A major aim of the research presented in this thesis was to use experimental designs that mirrored naturalistic settings. In doing so, the flexible way in which children learn has been highlighted. The field would benefit from continued development of paradigms that reflect children's learning environments. For example, studies may allow children (1) the opportunity to choose between personal exploration and requesting social information, (2) the opportunity to pick which models they do and do not source information from, before that information is provided and (3) to source further social information if and when they want it. Across species, it is important to maximise ecological validity in experimental research and experiments involving wild

natural open-diffusion designs encourage this (Kendal, Galef & van Schaik, 2010).

Research using artificial fruits in an open-diffusion design has been conducted in the wild with several species (Reader & Biro, 2010). However, the diminishing population of wild chimpanzees and the natural environment of the majority of chimpanzees (Goodall, 2000) create significant practical implications. A compromise may be to investigate social learning in semi wild chimpanzee populations.

Understanding Potential Applications

As mentioned previously, there is potential for the findings in this thesis to be applied to educational environments. As Gopnik (2012, p. 1623) asks in relation to children's learning, 'what is the ideal balance between individual discovery and learning from others, and does this balance shift in different educational and scientific contexts?' The role of prior experience seems extremely important in the acquisition of subsequent socially demonstrated behaviour. Educational establishments could benefit from the dissemination of this research. For example, allowing students to interact with an artefact (or problem) before direct instruction might increase that individual's overall knowledge of the challenge and reduce the reproduction of demonstrated irrelevant components. Additionally, educational institutions could benefit from an understanding that presenting different sources of information may not cause confusion but instead increase domain knowledge as has been found in approaches to mathematical problems (Siegler & Opfer, 2003).

Understanding the effect of model characteristics on high-fidelity copying is also pertinent in educational settings. Teachers are, generally, adults and prestigious and have demonstrated past-proficiency. Thus, they can transmit extremely useful information. However, their characteristics could result in such high fidelity copying

that some non-efficient elements of their behaviour also become transmitted. For children to think critically about a task, or a subject, there may be contexts where it is more fruitful to present multiple sources of information from a variety of models.

Potentially there are also ways in which this research can be applied to chimpanzee conservation. First, the conservation education benefit of revealing the cognitive abilities of chimpanzees (whether wild or captive) may go some way to ameliorating the threats faced by wild chimpanzees. Second, Whitehead (2010) argues that social learning could be important factors in translocation success. Thus, our increasing understanding of learning mechanisms and model-based biases in chimpanzee learning could assist with the potential reintroduction of groups into the wild. For example, we know that behaviours can be seeded into a group in the wild (meerkats; Thornton, & Malapert, 2009, orang-utans; Custance, Whiten, Sambrook, & Galdikas, 2001) and the evidence is beginning to suggest that particular individuals may be better at transmitting that information to a group (Biro, Inoue-Nakamura, Tonooka, Yamakoshi, Sousa, & Matsuzawa, 2003; Kendal et al, in prep). Therefore, training the correct models to perform species specific behaviours could increase the probability that these behaviours are adopted.

Conclusions

The body of work presented in this thesis further demonstrates that social learning is not best viewed as a binary variable of absence or presence. Instead, social learning encapsulates a spectrum of social learning mechanisms which will be influenced by social learning strategies. This thesis has married theoretical perspectives of cultural evolution with empirical research investigating chimpanzees' and children's learning. It has been demonstrated for the first time that chimpanzees' behaviour may be

guided by a sophisticated past-proficiency model-based bias. Likewise, it was found that children are flexible social learners that are able to adopt a number of model-based biases, use different social learning mechanisms in different contexts and are motivated to acquire adaptive additional information pertaining to a task. Alongside high fidelity copying, this motivation to acquire multiple methods, particularly after pertinent social information, could be influential in our species' reliance on cumulative culture. Both species show model-based transmission biases or 'who' social learning strategies, show flexible solution choice and are able to implement different learning mechanisms in different contexts. Differences between children and chimpanzees' learning strategies may lie in differences in reliance on various learning mechanism and transmission biases. This area is ripe for further exploration.

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